INSECT OAK DEFOLIATORS PARTITION SEASONAL TIME ON A MEDITERRANEAN MOUNTAIN

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Abstract

The insect eaters (chewers) of oak foliage were studied on a Mediterranean mountain where deciduous oaks coexist with evergreen oak species. We found 58 insect species (mainly Lepidoptera) in 20 families. These insects chewed the leaves of 8 *Quercus* species. The overlap in time and in feeding niche of the insects was examined by the: (a) Poole-Rathcke method, which tests phenological overlap and (b) Petraitis method. The main findings were:

1. It was found that insect families partition seasonal time in a random way.
2. Insect species formed 6 major feeding groups on the basis of the *Quercus* species exploited as feeding substrate, and individually these species are randomly distributed within the period of a year.
3. On the other hand the insects were found to share time in a variety of ways, which indicates that the overlap in feeding resources is compensated either by regular or random partitioning of time.
4. The hypothesis of complete general overlap is rejected for the different groups of feeding specialization and zoogeographical categories.
5. In a temporal sense only holarctic species partition time in a non-random way.
6. The specific niche overlap among insects is highly asymmetrical.
7. Food specialists were found to have random phenologies unlike the other specialization groups. In addition they have smaller dispersion ratio than the other specialization groups. Presumably this is used by small groups to relax high overlap.

• The entire assemblage partitioned time in a regular way (D_r = 4.16, $P < 10^{-3}$).

The overall conclusion is that in the oak foliage insect feeding guild the spatial overlap is compensated by a regular or random time partitioning. This work shows that the details of time partitioning are affected by the geographical distribution and feeding specialization of insect members.

where

Fig. A1 Map of Greece and adjacent countries.

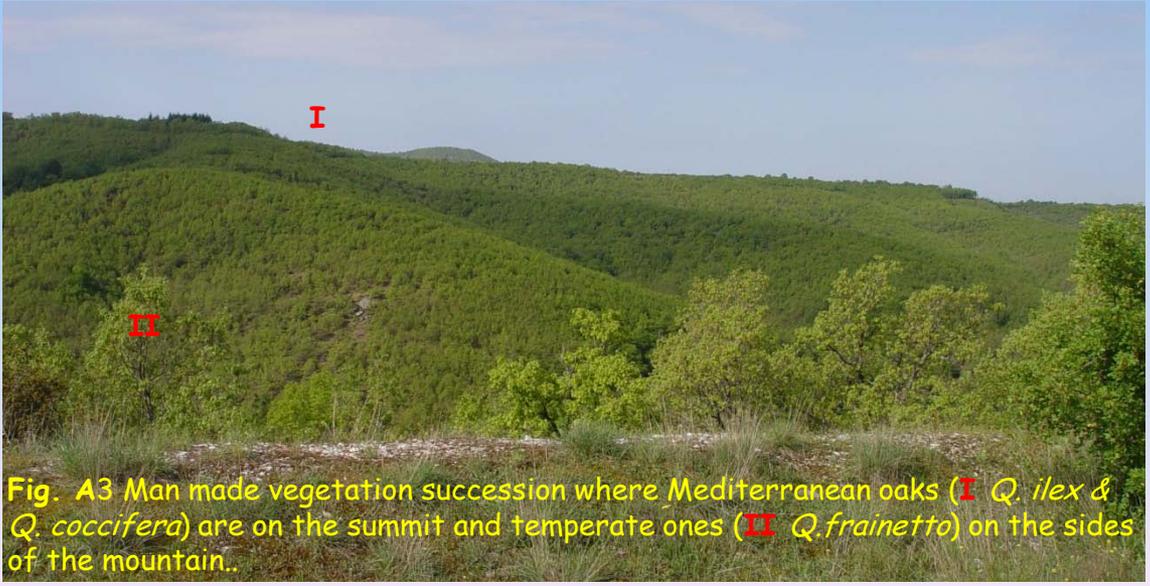Fig. A2 Representative landscape of the study area (Mt Holomontas, Chalkidiki, Greece).

Fig. A3 Man made vegetation succession where Mediterranean oaks (I *Q. ilex & Q. coccifera*) are on the summit and temperate ones (II *Q. frainetto*) on the sides of the mountain..

Fig. A4 Natural regeneration process on the forest floor (seedlings of *Fagus orientalis*).

how

Altitudes (masl)

< 100m

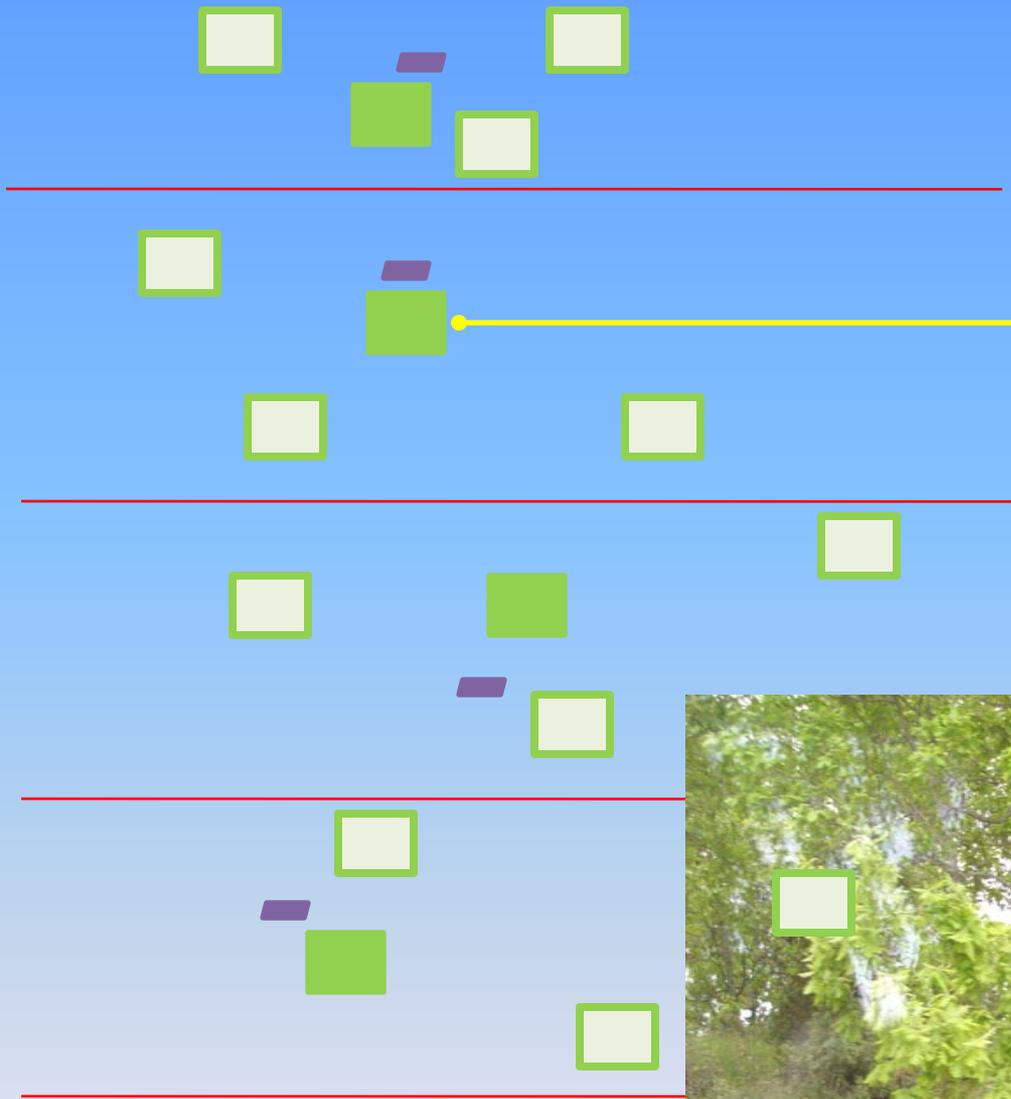100-250m

250-550m

>850m

sheltered place for selected insect species

2 ha base plot

2 ha plot

Plant coverage was measured for each species by means of the photographic technique of Aber (1979)

Insects were sampled by
1. Hand collecting (sleeves on branches, soft tweezers, aspirator)
2. Beat tray
3. Mistblowing employing an insecticide (C-permethrin) on the entire crown of 2 trees in each oak species (once a year)
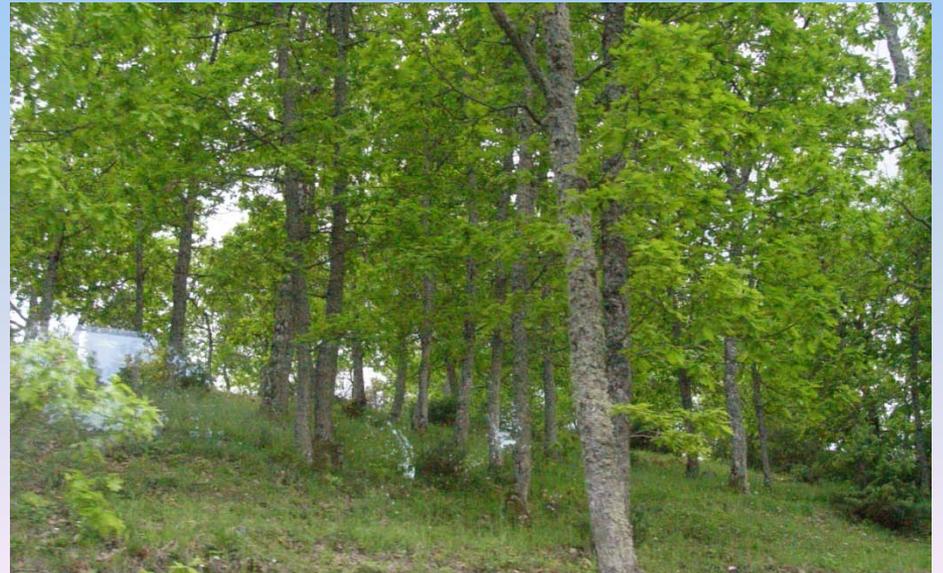
1 and 2 was performed in three tree heights (midpoints at 1.5, 2.5, 4 m)

Selected insect species for phenological observations, were reared in nearby sheltered places and their pupae were protected from natural enemies. Pupae protected (from natural enemies) in vials are shown in the photo.
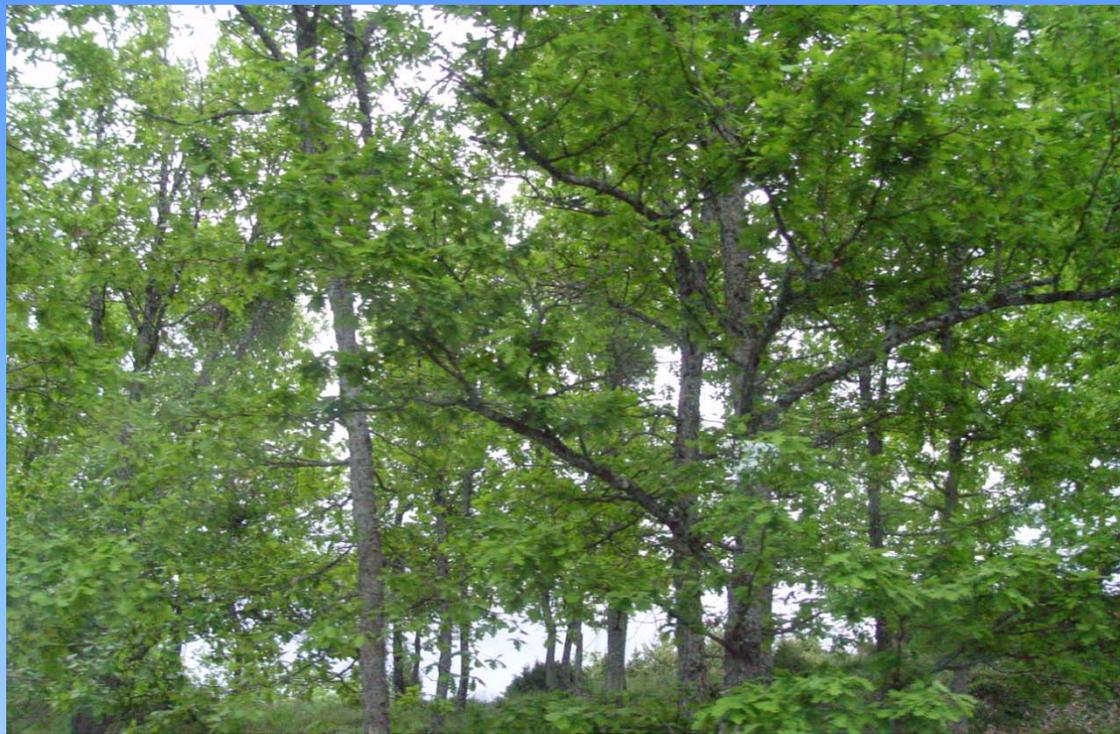
Aspect of two plots

Measurement and testing time segregation in insects

Poole-Rathcke method (1979; Rathcke 1984 and Rabinowitz et al., 1981)

▶ This method has been recently used by Pavon & Briones (2001) to study the distribution of flowering and fruiting peaks of perennial plants in a semi-arid scrub.

▶ To use the method in this study we treated the generations of insects as separate species.

Measurement and testing of niche overlap in insects

Petraitis method (1979, 1985)

▶ This method estimates the specific and general overlap of insect species and takes into account the exploitation of resources (here insect abundances on oak species coverage).

▶ It is designed to provide asymmetries in niche overlap between insect species (Denno et al., 1995).

▶ However the test it provides is only against complete overlap <u>not</u> against some overlap.

We found (handwritten annotation)

TABLE 1. Oak species found on Mt Holomontas and used in this study. The taxonomic section and growing status was taken from *Flora Europaea* (Schwarz 1964) and from personal observations (KM and PVP). Plant cover classes are in the Domin scale (Van der Maarel, 1979).

Oak species (*Quercus*)	Taxonomic section	Growing status	Plant cover classes	Bud burst
frainetto Ten.	Quercus	native	8	late March
dalechampii Ten.	Quercus	native	2	late March
pubescens Willd.	Quercus	native	4	early-mid April
ilex L.	Sclerophyllodrys	native	2	late April - late May
coccifera L.	Sclerophyllodrys	native	3	mid April – late May
trojana Webb	Cerris	planted[1]	1	mid March
macrolepis Kotschy	Cerris	native	2	mid March
robur L. subsp. pedunculiflora (C. Koch)	Quercus	planted[1]	2	late March

[1]Because the species is planted from seeds collected in neighboring areas the oak forest is characterized seminatural

TABLE 2. Listing of insect species found in the study plots on Mt. Holomontas. The specialization status was deduced from literature records (Schwenke 1978) and personal observations.

Family	sn	Species	Feeding specialization	Zoogeographical category
		Lepidoptera		
Cymatophoridae	1	*Polyploca ruficollis* Fabricius, 1787	m2	ES
	2	*P. ridens* Fabricius, 1787	m2	Med
Drepanidae	3	*Drepana binaria* Hufnagel, 1767	o1	Med
	4	*Cilix glaucata* (Scopoli, 1763)	p1	Med
Gelechiidae	5	*Anacampsis disquei* Mess, 1907	m2	Med
Geometridae	6	*Operophthera brumata* Linnaeus, 1758	p1	Pal
	7	*Alsophila aescularia* Denis et Schiffermuller, 1775	p1	Pal
	8	*Agriopis leucophaearia* Denis et Schiffermuller, 1775	m2	Pal
	9	*A. bajaria* Denis et Schiffermuller, 1775	o3	ES
	10	*A. marginaria* Fabricius, 1777	p1	Med
	11	*Erannis defoliaria* Clerck, 1959	p1	Pal
	12	*Biston strataria* Hufnagel, 1767	p1	Med
	13	*Collotois pennaria* Linnaeus, 1761	o3	ES
	14	*Cyclophora punctaria* Linnaeus, 1758	o3	ES
	15	*Apocheima pilosaria* Denis et Schiffermuller, 1775	o3	ES
Lasiocampidae	16	*Malacosoma neustria* Linnaeus, 1758	p1	Pal
	17	*Eriogaster catax* Linnaeus, 1758	o3	ES
Lycaenidae	18	*Quercusia quercus* Linnaeus, 1758	o3	Pal
Lymantriidae	19	*Porthetria dispar* Linnaeus, 1758	p2	Pal
	20	*Porthesia similis* Fuessly, 1775	p1	Pal
Noctuidae	21	*Bena prasinana* Linnaeus, 1758	o2	Pal
	22	*Orthosia cruda* Denis et Schiffermuller, 1775	o3	ES
	23	*O. stabilis* Denis et Schiffermuller, 1775	o3	Pal
	24	*O. miniosa* Denis et Schiffermuller, 1775	p1	Med
	25	*Cosmia pyralina* Denis et Schiffermuller, 1775	o3	Pal

Table 2 cont'd

	26	*Dicycla oo* (Linnaeus, 1758)	m2	ES
	27	*Agrochloa helvola* Linnaeus, 1758	m3	Pal
	28	*Minutia lunaris* Denis et Schiffermuller, 1775	m3	Med
	29	*Catocala nymphagoga* Esper, 1787	o1	Pal
	30	*Catephia alchymista* Denis et Schiffermuller, 1775	o1	ES
Nolidae	31	*Meganola strigula* Denis et Schiffermuller, 1775	o3	Med
Notodontidae	32	*Phalera bucephaloides* Ochsenheimer,1810	m2	Med
	33	*Spatalia argentina* Denis et Schiffermuller, 1775	o3	Med
	34	*Drymonia querna* Denis et Schiffermuller, 1775	o3	Pal
Nymphalidae	35	*Nymphalis polychloros* (Linnaeus, 1758)	p1	ES
Oecophoridae	36	*Carcina quercana* Fabricius, 1775	o3	Pal
	37	*Diurnea fagella* Hubner,1796	p1	Pal
Pieridae	38	*Aporia crataegi* (Linnaeus, 1758)	o3	Med
Psychidae	39	*Pachytelia villosella* Ochsenheimer, 1810	p2	Med
Pyralidae	40	*Acrobasis tumidella* Zincken, 1818	m2	Pal
	41	*A. consociella* Hubner,1910-13	m2	ES
	42	*A. sodalella* Zeller, 1848	m2	ES
	43	*Phycita spissicella* Fabricius, 1776	o3	Pal
Thaumetopoeidae	44	*Thaumetopoea processionea* Linnaeus, 1758	m2	ES
Tortricidae	45	*Tortricodes alternella* Denis et Schiffermuller, 1775	o3	ES
	46	*Tortrix viridana* Linnaeus, 1758	o3	Pal
	47	*Choristoneura sorbiana* Hubner, 1799	o3	Pal
	48	*Ptycholoma lecheana* Linnaeus, 1758	p1	ES
	49	*Zeiraphera isertana* Fabricius, 1794	o2	Pal
	50	*Archips xylosteana* Linnaeus, 1758	p1	ES
	51	*A. podana* Scopoli, 1763	p2	ES
	52	*Acleris literana* Linnaeus, 1758	m2	ES
	53	*Aleima loeflingiana* Linnaeus, 1758	p1	ES
Yponomeutidae	54	*Ypsolopha sylvella* Linnaeus, 1758	m2	ES
	Coleoptera			
Curculionidae	55	*Attelabus nitens* (Scopoli, 1763)	p2	ES
	Hymenoptera			
Tenthredinidae	56	*Caliroa annulipes* (Klug, 1816)	o3	ES
	57	*Periclista lineolata* (Klug, 1816)	m2	ES
	58	*P. albida* (Klug, 1816)	m2	ES

Symbol	Zoogeographical category	(Josifov 1986)
Med	Holo-mediterranean and North Mediterranean including those distributed up to Central Europe and ponto-mediterranean species	
ES	European and Siberian species (includes those occurring only in the west, east, north and montane ranges)	
Pal	Species covering the entire palaearctic region	

| Symbol	Special ization type (Jolivet 1998)	Insect leaf phytopages found	Biological meaning
m1	first-degree monophagy	0	feeds only on one species
m2	second -degree monophagy	16	feeds on several related species in a genus, usually within a taxonomic section (e.g. *sectio*: Sclerophyllodrys, genus: *Quercus*)
m3	third-degree monophagy	2	feeds on all species of a genus; it is also referred as generic monophagy
o1	first-degree oligophagy	4	feeds on related plants in several genera of the same family; sometimes the feeding is limited to one or several subgenera or sections of the same genus
o2	second -degree oligophagy	2	feeds on several genera in the same order (e.g. Fagales)
o3	third-degree oligophagy	22	feeds on a wide variety of plants in different orders of the same class but still have a specific trait in common (e.g. a chemical category of compounds such as the glucosinolates of Cruciferae and Tropaeolaceae)
p1	first-degree polyphagy	14	feeds on a variety of plants in different orders of the same class
p2	second-degree polyphagy	3	feeds on a variety of plants in several classes
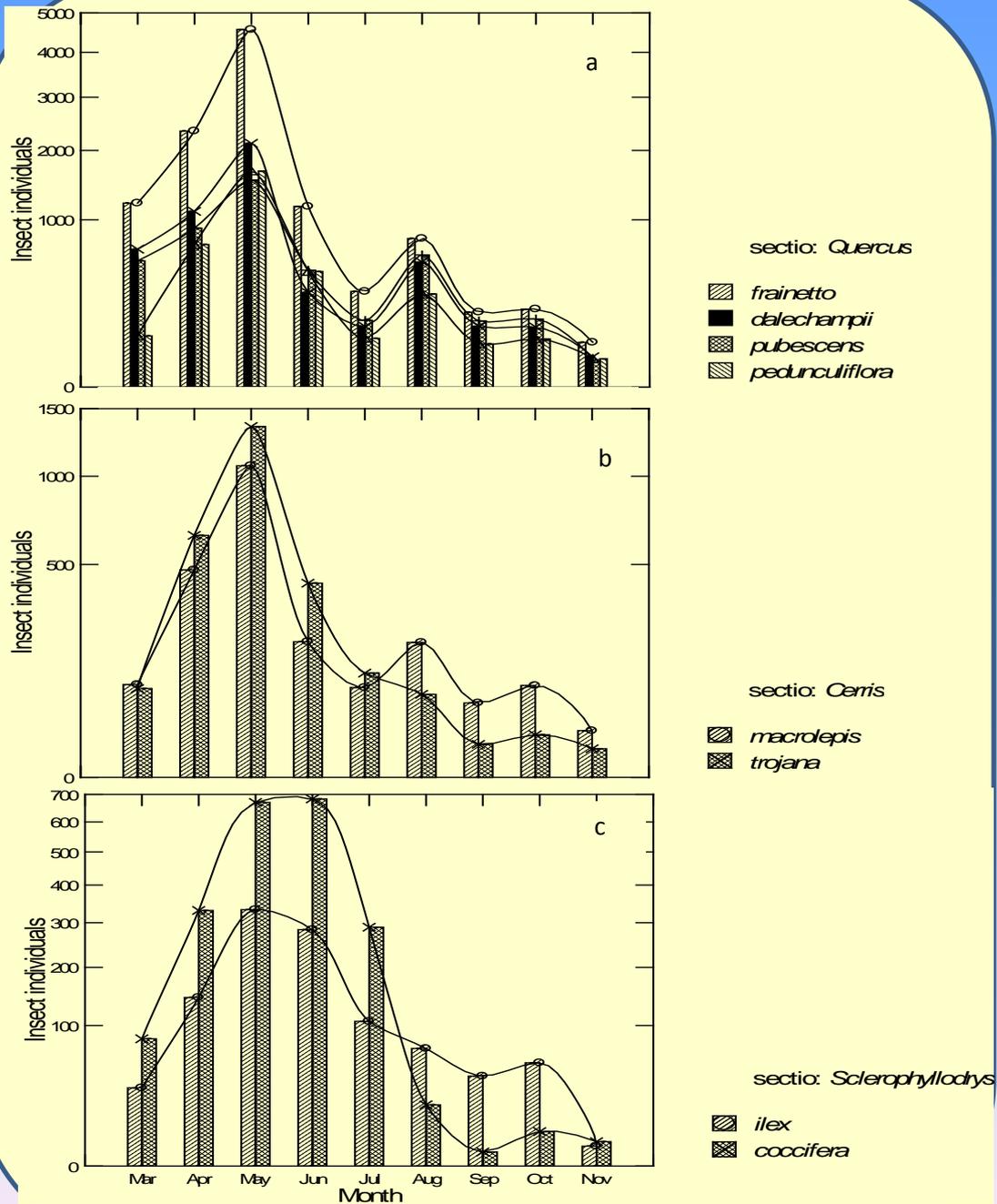
Fig. 1. Foliage chewer insect abundances in monthly intervals for each *Quercus* species. Square root data are presented to adequately show low abundances. The tops of the bars are connected with a smooth curve (spline interpolation) to reveal seasonal trends in insect abundances. The three plots correspond to the three taxonomic sections of the genus, **a**: section: *Quercus*, **b**: section: *Cerris*, **c**: section: *Sclerophyllodrys*.

Fig. 2. Classification of oak species according to the presences/absences of foliage insect species chewers. Insects from all months were used. The clustering method is UPGMA of Ochiai binary similarity coefficients (Hammer & Harper, 2006). Taxonomic sections in the genus *Quercus* are written in the boxes at the clustering nodes. ..
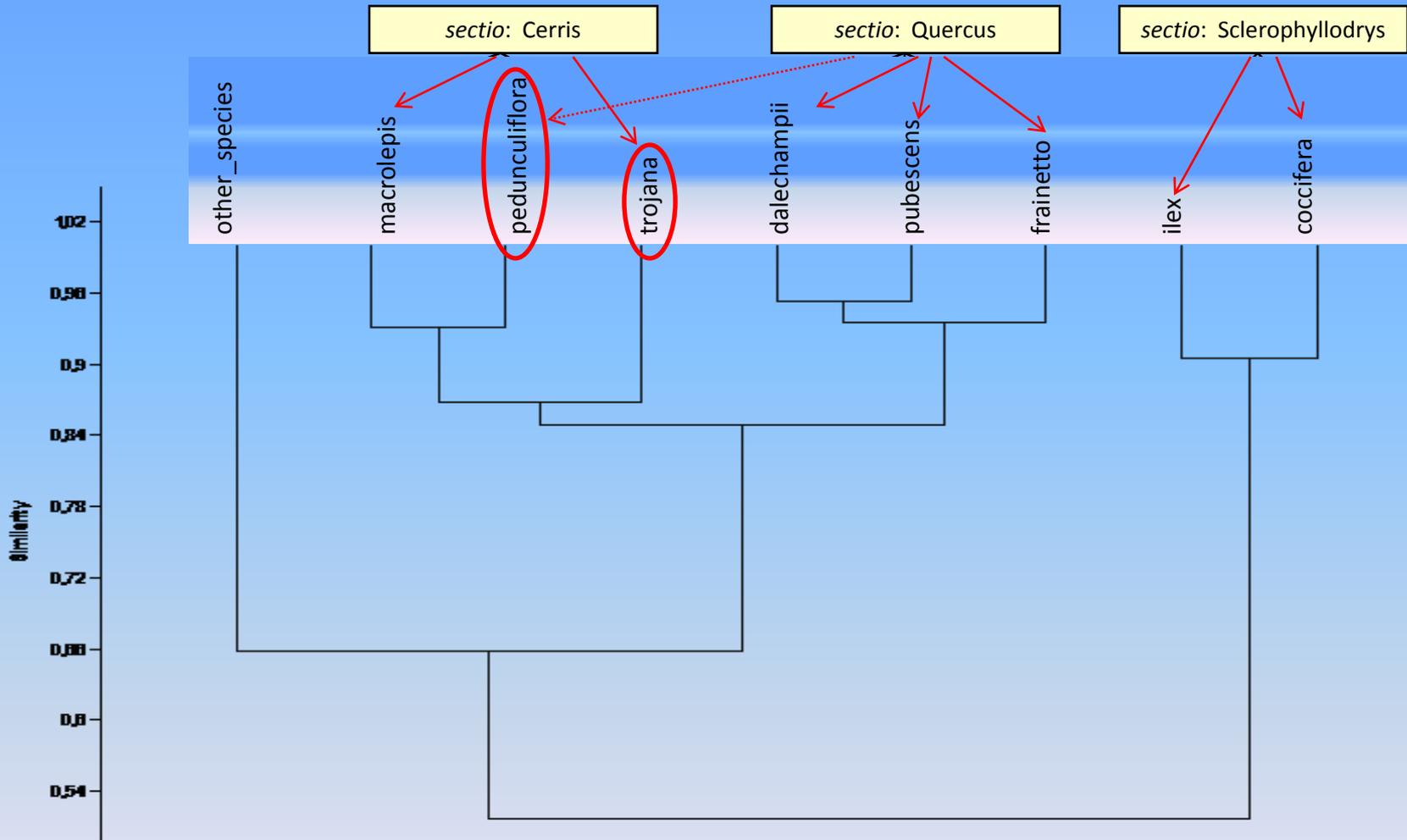
Introduced (planted) oaks (*Q. robur* subsp. *pedunculiflora* and *Q. trojana*) are circumscribed by ellipsoids. Only *Q. robur pedunculiflora* is clustered in another section closely to *Q. macrolepis*.

TABLE 3. Presentation of the results of the Poole-Rathcke method of time segregation of moths. The null hypothesis (H_{01}) states that the dispersion (Dr) is not significantly different from random, and the second null hypothesis (H_{02}) states that the two dispersions are not significantly different. Panel [a] is for insect families, [b] is for feeding specialization and [c] for biogeographical categories. When the second group is not explicitly written, the entire insect assemblage is meant.

[a]

Family	Number of species[1] [k]	Observed variance (×1000) [P]	Expected variance (×1000) [E(P)]	Dispersion ratio [Dr = P/E(P)]	Random dispersion (significance of H_{01})
Geometridae	11	3	70	0.036	ns
Noctuidae	10	19	76	0.254	ns
Tortricidae	10	41	76	0.538	ns
Insect assemblage	63	63	0.015	4.161	*** [2] ◄

[1] When more than one generation, exist the second generation is considered as a separate species
[2] In all panels, * corresponds to probability 0.05, ** to 0.01, and *** to < 0.001. Statistically weak results in other families are not shown

[b]

Feeding specialization	k Number of species[1]	P Observed variance (×1000)	$E(P)$ Expected variance (×1000)	$Dr = P/E(P)$ Dispersion ratio	Random dispersion (significance of H_{01})
m	18	0.42	2.74	0.153	ns
o	28	1.11	820.28	0.001	ns
p	17	0.52	2.76	0.188	ns

Feeding specialization compared	$Fs = Dr_1/Dr_2$	Same distribution (significance of the H_{02})
m-o	113.3	***
m-p	0.814	ns
o-p	0.007	ns

[c]

Zoogeographical categories	k Number of species	$Dr = P/E(P)$ Dispersion ratio	Random dispersion (significance of H_{01})
Med	21	0.315	ns
ES	24	0.144	ns
Pal	13	0.370	ns

Feeding specialization compared	$Fs = Dr_1/Dr_2$	Same distribution (significance of the H_{02})
Pal-ES	2.569	*
Pal-Med	1.176	ns
ES-Med	0.459	ns

TABLE 4. Specific niche overlap (*SO*) of oak foliage -eating insects within the various categories of feeding specialization and the zoogeographical categories which are combined in two large groups of distribution.

	Number of species	Number of significant *SO*s[1]	% of all specific overlaps (*SO*s)	% asymmetrical significant specific overlaps (*SO*s)
Feeding specialization				
m	16	33	13.8%	6.1%
o	24	11	2.0%	**27.3%**
p	21	4	0.3%	-
Zoogeographical categories				
ES + Pal	24 + 21	12	0.6%	**25.0%**
Med	13	24	15.4%	8.3%

TABLE 5. General, adjusted and minimum (*Gmin*) niche overlap within the various classes of feeding specialization and zoogeographical categories. The hypothesis H_0 states that the overlap among species is complete

	General overlap	Gmin	Adjusted general overlap	H_0
Feeding specialization				
m	0.545	0.090	0.500	**rej**
o	0.583	0.058	0.558	**rej**
p	0.483	0.068	0.445	**rej**
Zoogeographical categories				
ES	0.483	0.045	0.458	**rej**
Pal	0.505	0.061	0.473	**rej**
Med	0.412	0.079	0.362	**rej**

Fig. 3. Histogam of Petraitis' specific overlap measures (SO) of insect species. Each plot is specific to a feeding specialization type.
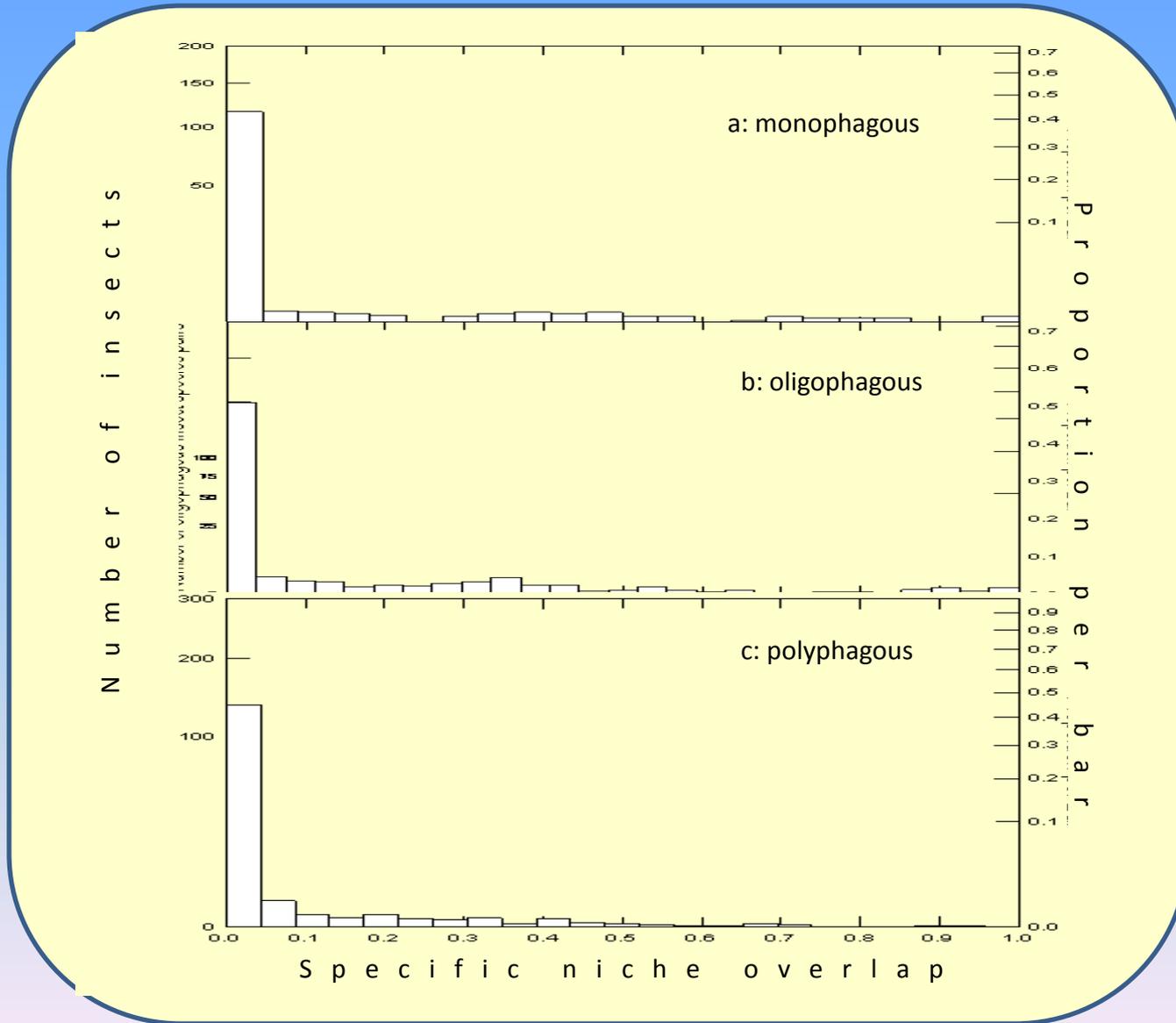
Fig. 4. Dendrogram showing the hierarchical Ward clustering of oak foliage eating species according to their niche specific overlap computed without taking into account the seasonal time. The six recognized clusters (see text for details) are marked with Arabic numbers (1...6). All species are denoted with the first four letters of genus and species names. Species "Acro co(2", "Cycl pu(2" and "Mega st(2" (red arrows) correspond to the second generation of *A. consociella*, *C. punctaria* and *M. strigula* with a changed host tree species. The scale at the right represents Euclidean distances (x1000).
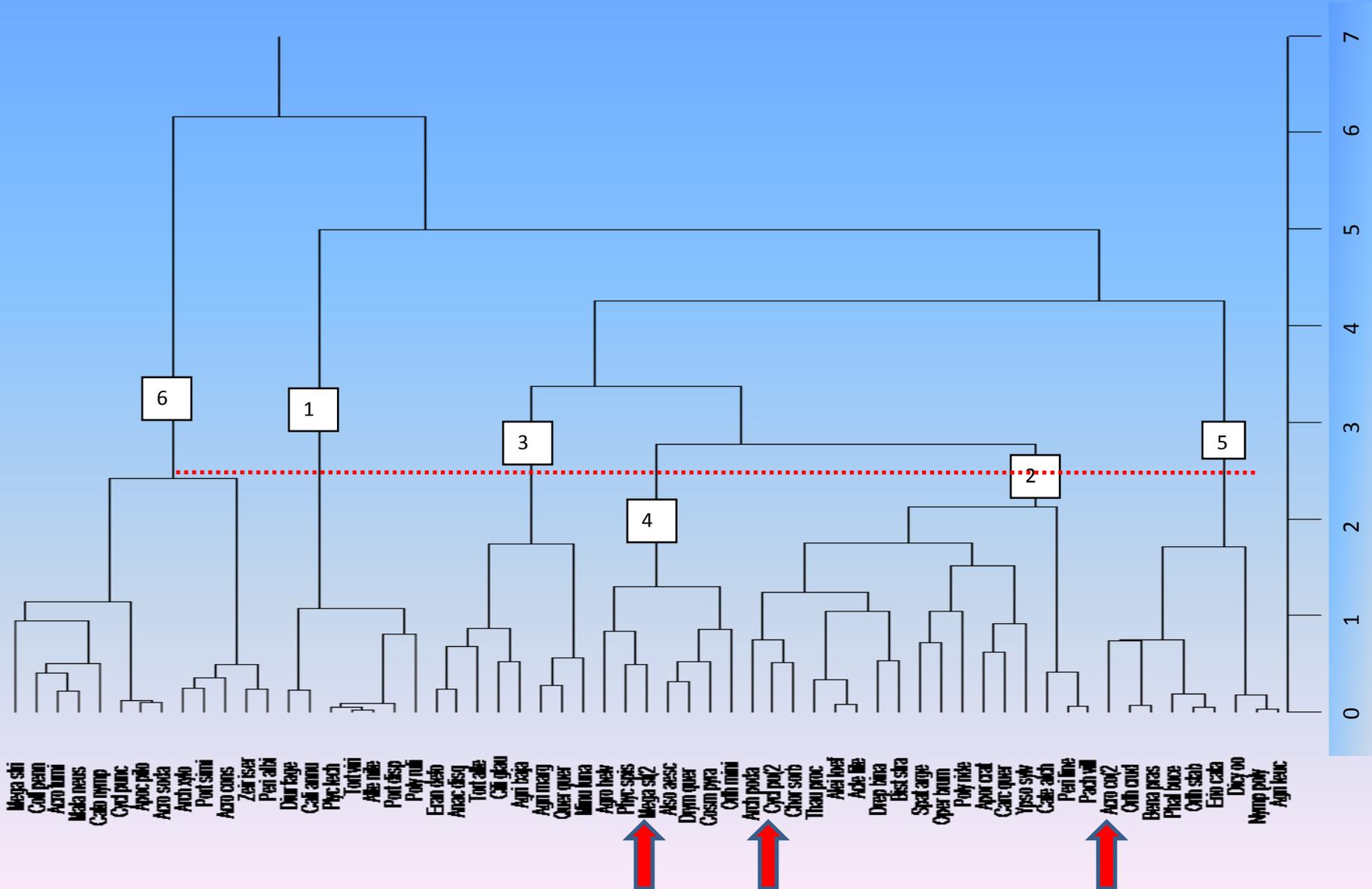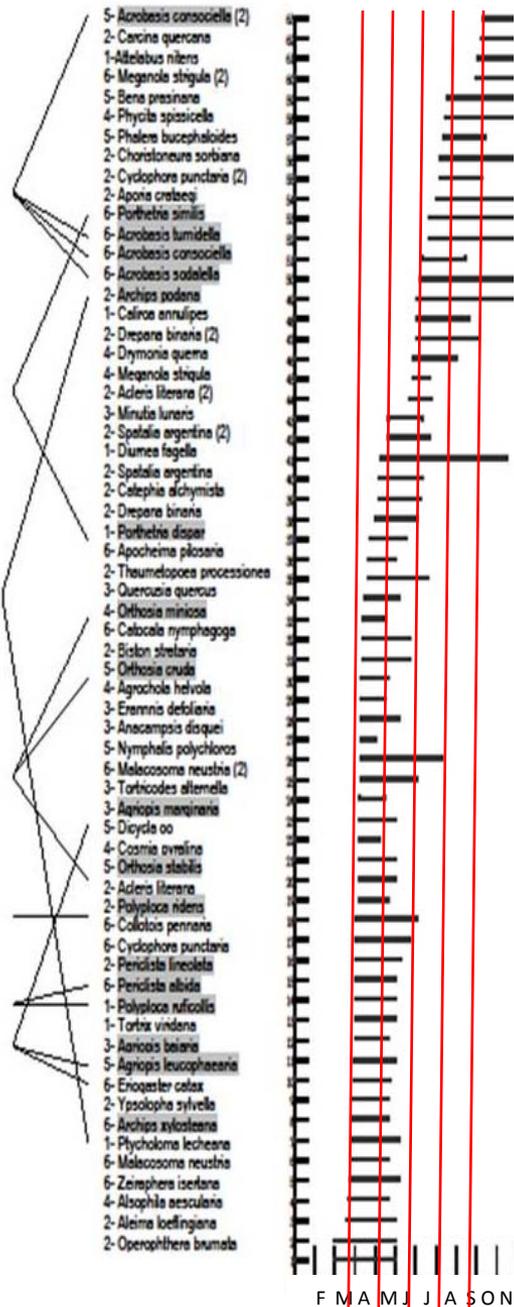
Fig. 5. The larval periods of the insects feeding on the leaves of oaks on Mt Holomontas are shown classified according to the peak of their appearance. Insects with two generations are shown as different species followed by the number '2'. Insect names are preceded with the affiliated cluster name marked with Arabic numbers (1...6).

Cilix glaucata (Lep., Drepanidae) is not shown because of the scarcity of its larvae. Instead, the insect is represented by *Periclista albida* (Hym., Tenthredinidae), which has the same starting and ending days of appearance.

Congeneric species are shown in grey background and are linked with convergent line segments.

The red vertical lines are drawn for convenience.

TABLE 6. Wald-Wolfowitz tests of the larval phenologies (mean of start and end date) of oak foliage feeding insect clusters. An insignificant test (*P* > 0.05) implies that larval phenologies of the insects belonging to the same cluster are randomly dispersed in seasonal time.

Cluster of *Quercus* foliage eating insects	*z* statistic	Two-tailed[1] *P*
1	-0.293	0.769 ns
2	-0.466	0.642 ns
3	-1.613	0.107 ns
4	-0.293	0.769 ns
5	0.604	0.546 ns
6	-1.006	0.314 ns

[1]because the absolute value of *z* is tested

TABLE 7 a.

Insect genera with more than one species are tabulated. The presence of a species in a cluster is represented by its number in this cluster and row sums represent the number of species in the respective genus. Exception is the second generation of *A. consociella* in cluster 5.

Cluster ▷	1	2	3	4	5	6
Genus ▽ (feeding type. | zoogeographical categ.)						
Acrobasis (m2,m2,m2| Pal,ES,ES)					1	3
Agriopis (m2,o3,p1 | Pal,ES,Med)			2		1	
Archips (p1,p2,m2 | ES,ES,ES)		1				1
Orthosia (o3,o3,p1 | ES,Pal,Med)				1	2	
Periclista (m2,m2 | ES,ES)		1				1
Polyploca (m2,m2 | ES,Med)	1	1				
Porthetria (p2,p1 | Pal,Pal)	1					1

Genus ▽ (feeding type. / zoogeographical categ.)		Cluster ▷ 1	2	3	4	5	6
A. consociella m2/ES	3 species in genus					←	●
M. strigula o3/Med	1 species in genus				←		●
C. punctaria o3/S	1 species in genus			●	→		→
D. binaria o1/Med	1 species in genus	←	●				
A. literana m2/ES	1 species in genus	●					
S. argentina o3/Med	1 species in genus	●					
M. neustria p1/Pal	1 species in genus						●

TABLE 8. Niche specific overlap of insect species with a second generation and comparison with the mean specific overlap of all insects . $\overline{SO}_{all} = 0.165$

Insect species	Hypothesis tested	Estimated specific overlap [*mean* ± *SD*]	*t*- value	*P*
		monophagous,		
❯ *Acrobasis consociella*		0.184 ± 0.300	0.357	0.362 NS
● *Acleris literana*		0.113 ± 0.188	-1.563	0.128 NS
		oligophagous,		
❯ *Drepana binaria*		0.223 ± 0.165	0.893	0.381 NS
❯ *Cyclophora punctaria*		0.080 ± 0.129	-4.775	$<10^{-4}$
❯ *Meganola strigula*		0.280 ± 0.228	2.874	0.006
● *Spatalia argentina*		0.183 ± 0.260	0.493	0.624 NS
		polyphagous,		
● *Malacosoma neustria*		0.106 ± 0.234	-1.476	0.075 NS

The second generation shifted feeding cluster ❯ yes
● no

Discussion 1/2

[**Fig. 1**] Three abundance peaks though the third peak in October is very low. The first peak in May extends to June in section Sclerophyllodrys and the second and third peaks exist only for *Q. ilex* and not for the fire adapted *Q. coccifera*. Southwood et al. (2004) believe that this section harbors a depauperate insect fauna as a result of evergreeness. The lack of second and third peaks is evident in *Q. trojana* but not in *Q. robur pedunculiflora* meaning that this is not related to the introduced status. In general the abundances are higher on oaks with a higher coverage. The Pearson correlations of insect abundances with the coverage of oak species are moderate though insignificant (r_1 = 0.685, r_2 = 0.839, r_3 = 0.731 NS for the three main peaks).

[**Fig. 2; Table 3**]   The insects (0/1) perceive well the three botanical sections of oaks with the exception of the planted *Q. robur pedunculiflora*. The section Sclero-phyllodrys is kept separate from other plants. Within each section insects cannot aggregate similar species as shown e.g. in the cluster Quercus (**Fig. 2**) where *Q. dalechampii* is grouped with *Q. pubescens* and not the taxonomically and geographically similar *Q. frainetto*. [**Fig. 2**] Moths are able to discriminate between *Quercus* taxa and prefer to lay eggs on these. In subspecific levels Simchuk (2008), on the basis of DNA techniques (RAPD-PCR data and OPA-14 primer) found that certain genotypes of *T. viridana* exhibit marginal fitness (fecundity and body size) on some certain genotypes of *Q. petraea* and *Q. pubescens* whilst show minimal fitness to other genotypes. In contrast, Tack et al. (2010) examining the insect herbivore communities of the oak *Q. robur* (miners, gallers and free feeders) found that the location of the tree is more important that its genotype or the interaction location X genotype. However, the only significant contribution to the little variation of insect community structure among genotypes was attributed to plant phenology (48%).

[**Table 4,5;   Fig. 3**]   All three families with enough species (to protect the power of tests) are randomly distributed in seasonal time. The entire assemblage consisted of all insect families exploiting time in a <u>non random way</u>. Feeding and geographical categorization gives similarly random temporal distributions. Nevertheless the mono- and oligophages together with Pal + ES share the seasonal time in different ways.

Even though monophages and Mediterranean insects show the highest percentages of significant overlaps the highest proportion of asymmetrical overlaps is exhibited by those categories showing low significant overlaps. These percentages are far lower than those reported by Denno et al. (1995). It seems that Mediterranean monophages tolerate packing. This ability disappears in the other categories (o- polyphages, Pal, and ES) since at least one member of an Specific Overlap couple is able to use other resources. This can be seen as inverse relationship between % of SOs and % of asymmetrical SOs. In term s of SOs among feeding types the prevailing amount is almost zero.

Discussion 2/2

[**Table 6; Fig. 4**]   On the basis of the values of niche specific overlap, oak foliage eating species and by means of a Ward joining algorithm, insects formed six recognizable clusters (**Fig. 4**). The recognition of feeding niche clusters was done by considering the first group met –cluster 6 in **Fig. 4**-– reading the dendrogram from the top. This group is "natural" according to McCune et al. (2002) because, after cluster 1, it is the first longest stem in the dendrogram. In addition, the *pseudo F* values peaked at this clustering level (SAS Institute, 2005) indicating that the level of six clusters is an acceptable one. Clusters were considered at this cutting level. The results of the Wald-Wolfowitz runs test for the statistical examination of the randomness of larval phenologies within each cluster are shown in **Table 6** and all clusters are shown to have random phenologies. Random larval phenologies indicate that there is no time structure within cluster.

[**Table 7a & b; Fig. 4**]   Insect genera with more than one species show the following pattern. All species of the same genus are affiliated to two clusters. The genera *Acrobasis*, *Agriopis* and *Orthosia* have the remaining species in one cluster. All insect species in all clusters are randomly distributed in seasonal time indicating that a more or less similar distribution on oak species marks a random spread in time. Another feature supports the same view. Four out of seven species that have a second generation exhibit a shift in feeding cluster (**Table 7b**). As a rule the shift is towards remote clusters according to the seriation provided in Fig. 4. In the same figure the mean distance of the shifts is *6.25* when the average distance of all clusters is *5.0*. The above indicate that the closer the species are in terms of phylogeny (congeneric species) the more probable it is to find one of them in another niche cluster. In the case of a second generation the shift to another oak tree species in the second generation is usually followed by a change in cluster membership (**Fig. 4**).

[**Table 8; Table 4 & 5**]   Bivoltine species having *SO* with the other insects less than *0.165* which is the mean *SO* of all insect species (**Table 8**) exhibit variable behavior in terms of cluster shift. The monophagous species *A. literana* does not show cluster shift while *A. consociella* with higher *SO* than *0.165,* in the second generation, moves to another cluster. In oligophagous insects *C. punctaria* with a very low *SO* (*0.080*) exhibits cluster shift while the remaining oligophages exhibit variable behavior. The polyphagous species *M. neustria* with *SO* lower than *0.165* does not exhibit a cluster shift.
In addition, the mean SO of insect feeding specializations decreases with decreasing specialization (**Table 8**). This pattern is not shown in the values of general overlap *GO* (**Table 5**). This indicates that species pairs relax specific overlap by diversifying their diet. If this diversification is unbalanced –*i.e.* exhibited by one member of the pair– then asymmetrical SOs are substantially more in oligophages (**Table 4**) and in species which are widely distributed –*i.e.* Palearctic and Eurosiberian.

The fact that only seven out of fifty-four moth species form a second generation can be explained by the pattern revealed by Cizek et al. (2006). Namely, quantitatively protected plants (like oak trees) host herbivores having reduced number of generations since their larvae are able to extend their growing window by digesting the nitrogen poor mature foliage. This pattern is not followed by noctuid moths which are present only in the leaf unfolding period. Presumably noctuids are unable to cope with the reduced nitrogen of mature leaves (Alonso and Herrera, 2000).

Conclusions

1. Insects discriminate among oak species either by means of leaf traits or phenology.
2. The study area is occupied by both temperate and Mediterranean *Quercus* species which exploit water in different ways and produce sugars and polysaccharides in different ways. Also there were all types of leaf shedding –i.e. evergreens, marcescent and deciduous- of oak trees (Ne'eman, 1993). The fact that *Q. pubescens* is principally deciduous but evergreen trees can be found in some places –usually means that it is the semi-evergreen subspecies *Q. p. brachyphylla*- which is reminiscent of the expected complications in the insect-plant ecology.
3. Insect abundances peak in May and August which are exploited by insectivores (ground beetles, tits and bats). The peak in May is mainly formed by noctuids that peak in May-June as long as new foliage exists. A peak in October is formed by those moths that overwinter as pupae or 2nd instar larvae.
4. Despite the fact that the entire guild of leaf chewers is non-randomly distributed in seasonal time
    i.   all three major families (Noctuidae, Geometridae, Tortricidae),
    ii. feeding specialization types (mono-, oligo-, and polyphages, and
    iii. biogeographical categories (Mediterranean, Eurosiberian, Palearctic)
    are random. The phenologies of the pairs (mono- and oligophages) and (Palearctic-Eurosiberian) are different. Whereas the difference of the members of the first pair can be explained on the basis of different strategies the P-E difference cannot be readily explained.
5. The feeding niche overlap set of insect species contains a high percentage of asymmetrical overlaps in accordance to the norm of Denno et al. (1995).
6. It has been stated that leaf chewing herbivores exhibit moderate interspecific competition. This pattern is found in this study but it is relaxed by means of temporal separation though not evidenced within taxonomic families, feeding specialization groups and zoogeographical categories.
7. Both deciduous (e.g. *Q. pubescens*) and evergreen oaks (e.g. *Q, ilex*) are very resistant in water stress and have equal water use efficiencies (Damesin et al., 1998 and references). However the first species but Q. ilex has higher internal resistance between CO_2 of stomatal chambers and chloroplast carboxylation sites. This ensures the continuity of nutrients (starch, soluble carbohydrates, nitrogen) throughout the year. Besides this Scleorphyllodrys harbors the least number of individuals and lowest richness among oaks. Possibly the pattern revealed by Bolz (2008) in central European oaks that after coppicing biodiversity decreases with time (in years) is more intense for Mediterranean evergreen oaks (Sclerophyllodrys).

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Thank you for your attention