



Biodiversity and microclimatic divergence of chrysomelid beetles at 'Evolution Canyon', Lower Nahal Oren, Mt Carmel, Israel

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Ninety species of leaf beetles (Chrysomelidae, Coleoptera, Insecta) were recorded from the 'Evolution Canyon' microsite (sample area 7000 m²), Lower Nahal Oren, Mt Carmel, Israel. Species richness was significantly ($P=0.018$) higher on the drier, climatically more fluctuating savanna-like, south-facing slope (SFS, 60 species, sample area 3000 m²) than on the cooler, wetter and climatically less variable north-facing slope (NFS, 44 species, sample area 3000 m²), as in other terrestrial taxa. More species were found common to the local xeric SFS at the Canyon and the regional southern desert areas (Judean and Negev Deserts), than to the NFS and Galilee Mountains, respectively, suggesting that local patterns mirror regional patterns. Interslope differences in microclimate variability range indicate that this factor might be determinant of interslope species richness differences. Most species were collected in the spring (April; 47%) and least in the autumn (September; 3%) over the collecting period from March 1995 to June 1997.

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CONTENTS

Introduction	140
Material and methods	140
Site	140
Sampling	142
Statistics	142
Results	143
Species richness: spatial and temporal diversity	143
Distribution of mono-, oligo- and polyphagous species	144
Qualitative interslope differences	145

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Discussion	145
Species richness and abundance	145
Temporal species distribution	146
Spatial species distribution	146
Conclusions	147
Acknowledgements	147
References	147
Appendix	149

INTRODUCTION

Despite the worldwide recognition of the great importance of studying, measuring, estimating and conserving biodiversity (e.g. Anonymous, 1992; Hawksworth, 1995; Heywood & Watson, 1995; Prance, 1995), we are still far from knowing the answers to basic questions, such as how many species have existed or currently exist on Earth (May, 1988; Ehrlich & Wilson, 1991) or what is the relative role of the deterministic, stochastic factors and history in the generation, maintenance and dynamics of biodiversity (Nevo, 1995, 1997a,b).

The present study is part of an interdisciplinary long-term study of biodiversity at 'Evolution Canyon' (henceforth the Canyon), Lower Nahal Oren, Mt Carmel, Israel (Nevo, 1995, 1997). The long-term objective of the project is to analyse determinants of species distribution, whether the global latitudinal trend in numbers of species (Schall & Pianka, 1978) might be demonstrated locally, the relative importance of stochastic and deterministic factors, and history of biodiversity differentiation and the processes that generate and maintain genetic diversity in nature. We are trying to answer these questions by analysing different groups across phylogeny (i.e. bacteria, lower and higher plants, invertebrates and vertebrates) (Nevo, 1995, 1997) to show possible underlying common patterns. Leaf beetles (Chrysomelidae) is the second beetle group studied so far at the Canyon, following darkling beetles (Tenebrionidae) (Chikatunov *et al.*, 1997).

Based on general expectations and our previous results we anticipated finding in the leaf beetles the following patterns of interslope differentiation:

- (1) Higher species richness on the 'tropical' south-facing slope (SFS) than on the 'temperate' north-facing slope (NFS). This prediction was tested at the Canyon microsite along with other terrestrial groups (Nevo, 1995, 1997; Chikatunov *et al.*, 1997) and paralleled the global pattern of general decrease of species richness from tropical to temperate latitudes (Schall & Pianka, 1978).
- (2) Higher number of 'xeric adapted' species on the drier and climatically more stressful SFS than on the opposite, climatically less fluctuating NFS. This prediction follows the more general expectation that warmer SFS should harbour more terrestrial, xeric 'tropical Asian and African' biota (Nevo, 1995).
- (3) More species active in the dry and hot summer period on the more humid and cooler shady NFS.

MATERIAL AND METHODS

Site

'Evolution Canyon', Lower Nahal Oren, Mt Carmel (32°43'N; 34°58'E) is a typical Mediterranean valley with a stream which is dry in summer at the bottom,

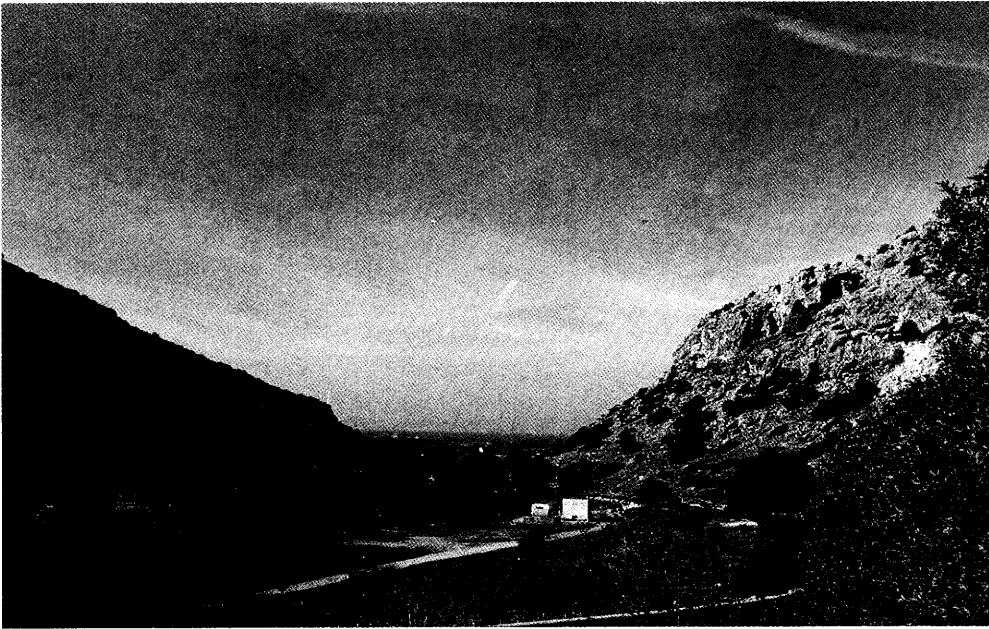


Figure 1. 'Evolution Canyon', Lower Nahal Oren, Mount Carmel, Israel. The warmer, less humid and climatically more fluctuating tropical 'savanna'-like south-facing slope (SFS) sharply contrasts with cooler, climatically more stable temperate north-facing slope (NFS).

and microclimatically sharply contrasting south-facing and north-facing slopes, as is clearly demonstrated by the sharp biotic contrast (Fig. 1). The canyon is presumably 3–5 million years old (Nevo, 1994, 1995), eroded from tectonically uplifted Upper Cenomanian limestone (Karcz, 1959), and geologically identical on both slopes. The interslope distance is 100 m at the bottom and 400 m at the top of the valley. The opposite slopes represent dramatic biotic contrasts and divergence due to the higher (up to 600% more in certain periods of the year) solar radiation on the SFS than on the NFS (Pavliček *et al.*, in prep.). The SFS is significantly warmer (average SFS/NFS temperatures representing 154 sample days over the 1997–98 period were 19.46°C and 18.55°C respectively; Wilcoxon test, $P=0.042$), significantly less humid (average relative humidity representing 173 sample days was 68.90% on SFS and 70.54% on NFS; Wilcoxon test, $P=2.10^{-5}$, respectively). Average daily difference between maximal and minimal temperature was significantly higher (Wilcoxon test, $P<1.10^{-6}$) on the SFS (11.36°C) than on the NFS (8.32°C). Likewise, average daily humidity difference was significantly higher on the SFS (41.75%) than on the NFS (34.40%) (Wilcoxon test, $P<1.10^{-6}$) (all humidity and temperature data from Pavliček *et al.*, in prep.). Therefore, the SFS receives more radiation, is warmer, less humid, with higher average daily humidity and temperature fluctuations and spatiotemporally represents a 'broader-niche' (Van Valen, 1965). The SFS dips 35° and is 120 m long, whereas the NFS dips 25° and is 180 m long (Nevo, 1997); the collecting area was about 1000 m² around each station (see below), totalling 7000 m² in the seven stations.

Sampling

Beetles were collected on each slope and from the bottom of the Canyon by sweeping with an entomological net, and *Cyrtanastes libanensis* was collected by pitfall traps (details in Chikatunov *et al.*, 1997). The beetles were collected twice each month from March 1995 to June 1997. Each slope was divided into upper (SFS1, NFS7; 120 m a.s.l.), middle (SFS2, NFS6; 90 m a.s.l.) and lower (SFS3, NFS5; 60 m a.s.l.) stations. To get as complete an inventory of the Canyon chrysomelids as possible, we also collected at the valley bottom (B4 station), although our predictions related only to interslope comparisons. Collections on the opposite slopes and stations were made on the same dates, and approximately at the same time of day (always in the morning). We spent the same collecting time (30 minutes) at each station on each collection date. One should be aware of possible sample bias due to interslope differences in vegetation (Nevo *et al.*, 1998). The same intensity of sweeping in an oak macquis on the NFS versus bushes and grasses on SFS might not mean the same effectiveness. Bias of this kind might have most effect on abundances and we therefore concentrated mainly on differences in species richness (the number of species per region; Heywood & Watson, 1995), which should be influenced less by any collection bias.

Severe disturbances of biota were caused by cattle grazing in April of both years at B4 and May of both years on SFS3 and SFS2.

Statistics

The Sign test was used for evaluation of pair inter- and intraslope differences in species richness. We did not use parametric tests, because we could not validate the normality distributions in our data sets. Due to our *a priori* prediction of higher species richness on the SFS than on the NFS, we anticipated a satisfactory α -level ($=0.10$) for rejection of the H_0 hypothesis.

To measure intersample complementarity (distinctiveness, distance) we employed the true metric Marczewski–Steinhaus complementarity index (C_{jk}), which has been shown to satisfy the triangle inequality (Levandowsky & Winter, 1971). The index was computed according to the formula as follows (Colwel & Coddington, 1994):

$$C_{jk} = \frac{\sum_{i=1}^{S_{jk}} |x_{ij} - x_{ik}|}{\sum_{i=1}^{S_{jk}} \max(x_{ij}, x_{ik})},$$

where x_{ij} and x_{ik} are the presence–absence (1,0) values for species i in the lists j and k .

To better evaluate some of the results over the entire collecting period (March 1995–June 1997) we chose two 12-month periods (March 1995–February 1996 and March 1996–February 1997) to see if the same trends were repeated or unique to a particular collecting period. The binomial test was used to evaluate differences in

TABLE 1. Percentage complementarity of leaf beetles among stations of 'Evolution Canyon'

	SFS1	SFS2	SFS3	B	NFS5	NFS6	NFS7
SFS1		0.67	0.68	0.77	0.76	0.86	0.89
SFS2			0.60	0.74	0.71	0.85	0.93
SFS3				0.56	0.73	0.65	0.86
B					0.72	0.83	0.85
NFS5						0.76	0.75
NFS6							0.82

SFS-NFS = 0.64.

species richness between two collection seasons; the H_0 hypothesis was that there is equal probability for each species to be caught in the first or second collecting season.

RESULTS

Species richness: spatial and temporal diversity

In the Canyon 90 species of chrysomelid beetles have been recorded (Appendix); 87 species were collected by us in a 2-year period, and three additional species were recorded from the entomological collection of Tel Aviv University (although they were not included in the intra- and interslope analysis of species richness). This number collected from the sample area of 7000 m² represents 20% of Israeli fauna of leaf beetles (Lopatin *et al.*, 1997). The number of species on the SFS ($n=60$) was significantly higher than on the NFS ($n=44$) by Sign test ($P=0.027$). Pairwise interslope comparisons showed a significantly (by Sign test) higher number of species on SFS stations than on the opposite NFS in SFS2-NFS6 (29 and 17 species, respectively, $P=0.059$), and SFS3-NFS5 (51 and 29 species, respectively, $P=0.02$) comparisons, but not in SFS1-NFS7 (23 and 16 species, respectively, $P<0.28$), although the trend was similar, i.e. higher species richness on SFS. Intraslope comparisons showed that species richness differences were significantly different between the middle and lower stations (SFS2-SFS3, $P=0.003$; and NFS5-NFS6, $P<0.038$ for SFS and NFS, respectively), but not between middle and upper ones (SFS1-SFS2, $P=0.32$; NFS6-NFS7, $P=1.000$). Species number on both slopes decreased with increasing height above the valley bottom. The highest number of species was found on the valley bottom (B4), and the nearby stations (SFS3 and NFS5).

The percentage of slope M-S complementarity was 64%, showing low species interslope overlap. Also, the interstation overlap was rather low. M-S complementarity ranged from 56% (B4-SFS3) to 93% (SFS2-NFS7) (Table 1). Not only was a higher species richness of leaf beetles characteristic for the SFS, but also a higher number of species per genus (2.1 on SFS and 1.9 on NFS, while the average was 2.3 species per genus) and a higher number of genera (29 genera on SFS and 23 genera on NFS).

In the first and second 12-month periods we collected respectively 34 and 40 species of leaf beetles at B, 46 and 51 species on the SFS, and 29 and 38 species

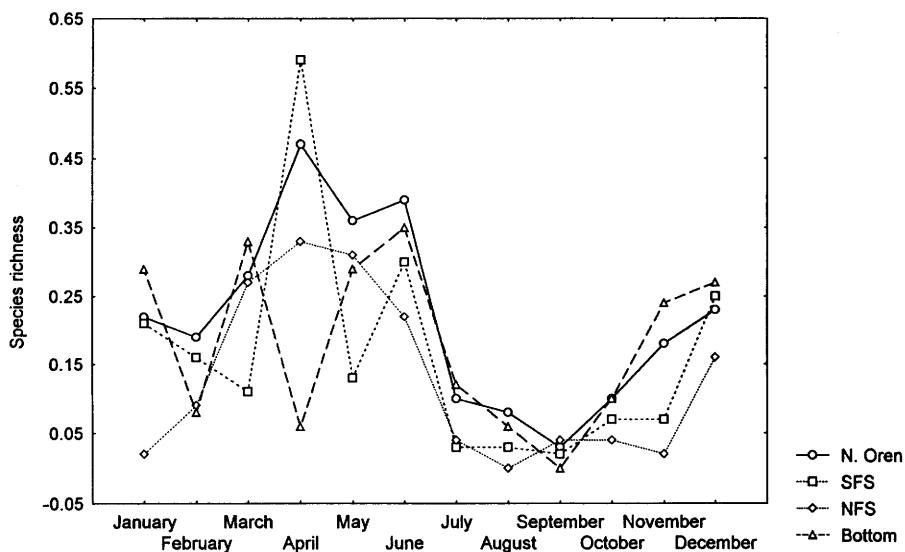


Figure 2. Distribution of species richness over the year at 'Evolution Canyon', Lower Nahal Oren, Israel.

on the NFS. In both collecting seasons species richness was higher on the SFS, and in the first collecting season the interslope difference was nearly significant by binomial test ($n=54$, $P=0.06$), but not in the second year.

From the beginning of March 1995 to the end of February 1996 we collected 54 species of leaf beetles, and in the equivalent time span from 1996 till 1997 we collected 68 species. Forty-two species (60%) were found in both 12-month periods; 12 species were only found in 1995/1996 and 26 only in 1996/1997. The difference between the two 12-month periods in the number of unique species was significant by a binomial test ($P=0.03$).

Mean abundance per species in the Canyon was 17.2 individuals and it was twice higher on the SFS (10.7) (median abundance = 4.0) than on the NFS (5.1) (median abundance = 2.0). At the seven stations average species abundance was as follows: SFS1 (3.52), SFS2 (4.55), SFS3 (8.60), B (11.55), NFS5 (2.66), NFS6 (5.00), NFS7 (4.19). There were intraslope clines of increasing abundance from SFS1 to SFS3 and from NFS5 to NFS7, thus revealing opposite clinal trends in species richness on opposite slopes.

On average, most species were active from March till June. In April we collected 47% of all species (Fig. 2). There was a very steep decline of species richness in the summer on SFS, NFS and bottom, with only three species active in the Canyon. Two species were found on the NFS, one on the SFS and none at the bottom of the valley. At the beginning of the new season, in January there seemed to be an interslope difference, with lower species richness on the NFS than on the SFS.

Distribution of mono-, oligo- and polyphagous species

Fifty-one percent (out of 80 species for which data about their host plant spectrum were available) of species collected at the Canyon were monophagous, 34% were

oligophagous and 15% were polyphagous (see Appendix for host spectrum of each species). The proportion of species originating in different biogeographical regions was: Mediterranean (0.42), Palaearctic (0.21), Eastern Mediterranean (0.14), Levantine (0.18), and Holarctic (0.03) (see Appendix for the global and regional species distribution). No significant interslope (or between the slopes and the bottom) differences were found in the abundance of different zoogeographical groups. We did find, as expected, a higher number of species adapted to the desert environment of southern Israel (Negev, Dead Sea area and Arava Valley) on the SFS (23) than on the NFS (16), but the interslope difference was not significant.

Qualitative interslope differences

Twenty species were significantly more abundant on one of the slopes, measured by two-tailed binomial test. On the NFS, significantly, only four species (9%) were more abundant: *Smaragdina viridana* ($P=0.004$), *S. limbata* ($P=0.016$), *Pachybrachis glycirhizae* ($P=0.004$), and *Dicladispa testacea* ($P<1.10^{-5}$). On the SFS 16 species (23%) were more abundant: *Coptocephala destinoi* ($P<1.10^{-5}$), *C. dahdah* ($P<1.10^{-6}$), *C. peyroni* ($P=0.022$), *C. egerickxi* ($P=0.016$), *Pachybrachis akbesianus* ($P=0.032$), *Cyrtanastes libanensis* ($P=0.016$), *Exosoma thoracica* ($P<1.10^{-5}$), *Marseulia dilativentris* ($P=0.008$), *Phyllotreta corrugata* ($P<1.10^{-5}$), *P. cruciferae* ($P=0.016$), *Longitarsus aeneus* ($P<1.10^{-5}$), *L. dabernardii* ($P<0.022$), *L. allotrophus* ($P=0.016$), *Psylliodes cuprea* ($P=0.004$), *P. hyoscyami* ($P=0.004$), and *Podagrica malvae saracena* ($P<1.10^{-5}$). Four significantly abundant species out of 44 on the NFS might be a result of type I error, but the probability that 14 significant species out of 87 on the SFS is a result of chance is $P=0.00009$ (binomial test). The proportion between significant species for the NFS and SFS ($4/16=0.25$) was almost three times higher than expected from the interslope differences in species richness ($44/60=0.73$).

DISCUSSION

Species richness and abundance

Significant differences in species richness between the NFS and SFS parallel the pattern found in other 'terrestrial' groups (defined as groups that do not need free available water for gamete fusion) such as plants, scorpions, fruit flies, reptiles, birds, rodents (see Nevo, 1995, 1997 for references) and tenebrionid beetles (Chikatunov *et al.*, 1997). Our local microsite interslope patterns parallel the higher species richness in the African savanna on the SFS and lower species richness in the temperate European lifezone on the NFS. This interslope species differential mirrors the global decrease of species richness from tropical to temperate regions (for example Schall & Pianka, 1978, Rosenzweig, 1992 and others). The Canyon is influenced by the Mediterranean regional climate, which is the same for both slopes, and therefore the interslope difference in species richness might be related to microclimate (e.g. solar radiation, temperature, and humidity). The amount of variability may be more important than average microclimate, extending the width of spatio-temporal 'climate niche' for species. If this variability is cyclical (or

predictable), then natural selection might be a driving force of establishing and maintaining higher species richness in spatio-temporally more variable environments, in a similar way as predicted temporally for establishing and maintenance of genetic variability by Kirzhner *et al.* (1995).

The number of species per genus in the Canyon was low relative to the proportion in Israeli leaf beetles (4.26 species per genus, Lopatin *et al.*, 2000). There are several possible explanations. Mt Carmel, surrounded by the coastal plain and the Yezreel Valley, may have 'island-like' characteristics. The species/genera ratio of leaf beetles calculated by Lopatin *et al.* (2000) for Mt Carmel generally showed a similar result to the Canyon (two species per genus), and was lower than the ratio calculated for other zoogeographical areas of Israel. If this pattern is real, we should expect it to be revealed by the species- (and genera-)area relationship in Israel, but there are as yet no comparable data. The low number of species per genus is unlikely to be due to different intensity of sampling in Israel as compared to the Canyon. In the Canyon we found one new monotypic genus (*Cyrtanastes*) and four species new to Israel and to science (Pavliček *et al.*, 1997, 2000). If this reflects a more general trend, then with greater sampling effort of leaf beetles all over Israel we may expect on average to increase the species/genera ratio in Israel.

Further extensive collection is needed to estimate species richness at a locality. We found 40% of all leaf beetle species during one collection season but none in the other. Additional species might be found if collecting continues for more years. This study has also contributed to the discovery of a species new to science (*Antipa* sp. nov., under description).

Higher abundance on the SFS parallel higher species richness, as predicted. The stations which contributed most to diversity were SFS3 and B4.

Temporal species distribution

Maximal species richness (computed over both years) in the Canyon was in April (47% of all sampled species) and the minimal estimate was in September (3% of all sampled species) (Fig. 1). The decline of species richness from June to September is very similar both on the slopes and at the bottom. There appeared to be very little leaf beetle activity on either slope from July to September. An interslope difference is apparent at the beginning of the season; in November and January relatively more species appear on the SFS and bottom than on the NFS, possibly because of its warmer weather conditions.

Spatial species distribution

The trend towards a higher number of desert species on the SFS than on the NFS was expected, and was found in other groups such as grasshoppers (Pavliček *et al.*, 1997, 2000), tenebrionid beetles (Chikatunov *et al.*, 1997), plants (Nevo *et al.*, 1999), and rodents (Blaustein *et al.*, 1996). An illuminating example of this trend is the only Arabian species we found in the Canyon, *Cryptocephalus egerickxi*. This species was hitherto known only from Arabia, including Jordan, and in the Canyon seven specimens were found on the SFS and three at the bottom of the valley. A higher proportion of species were significantly more abundant on the SFS than on the

NFS, which might indicate that habitat generalists are living on both slopes, but that habitat specialists prefer the SFS.

CONCLUSIONS

- (1) Species richness of leaf beetles was significantly higher on the more drier and climatically more fluctuating SFS than on the opposite more humid and shady NFS, as predicted.
- (2) More species common to the Canyon and the southern deserts were found on the SFS than on the NFS. This reflects local regional patterns, indicating the important role of species divergence at a microsite presumably reflecting climatic adaptations.
- (3) Our data indicate a sharp decline of species richness in summertime. In the second half of the summer only 1–2 active species remain on both slopes.

This work supported the idea that the local patterns of species richness differentiation might reflect the regional and global patterns. There are open questions concerning history and biogeography of the regional fauna. For example, does the higher abundance of Levantine species on the SFS than on the NFS reflect the regional pattern of speciation in the Levant? How is the pattern of local distribution of taxonomic diversity connected to the differences in genetic, morphological, physiological and behavioral characters of species? What is the relative role of biotic factors in our model? Is abiotic (climatic) selection the main driving force of biodiversity differentiation of leaf beetles?

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APPENDIX

List of leaf beetles (*Chrysomelidae*) collected from 'Evolution Canyon', their global and local distribution and host plant spectrum

Abbreviations: A - Arabian, B - bottom, EM - Eastern Mediterranean, H - Holarctic, L - Levantine, M - Mediterranean, Mp - monophagous, NF5, NF6, NF7 - lower, middle and upper stations on the north-facing slope, Op - oligophagous, P - Palaearctic, Pp - polyphagous, SF1, SF2, SF3 - upper, middle and lower stations on the south-facing slope, TAU - entomological collection of Tel Aviv University.

Species	Distribution										Host spectrum						
	L	EM	A	M	P	H	SF1	SF2	SF3	local B	NF5	NF6	NF7	Mp	Op	Pp	
SUBFAMILY ORSODAGNINAE																	
<i>Orydoacene lineola ruficollis</i> Pic, 1894	X					X				3			3		X		X
<i>Zagophora scutellaris</i> Suffrian, 1840										2							
SUBFAMILY CRIOCERINAE																	
<i>Crioceris asparagi</i> Linné, 1758				X						1	1			X			
<i>C. bicruciatata</i> Sahlberg, 1823				X						1				X			
<i>Lilloceris faldernmanni</i> Guerin-meneville, 1844			X							1	1			X			
<i>Oulema melanopa</i> Linné, 1758				X				1	2	5	7						X
SUBFAMILY CLYTRINAE																	
<i>Labidostomis diversifrons</i> Lefevre, 1872			X							1							X
<i>L. decipiens</i> Falderman, 1837			X					2	11	2							X
<i>Antipha macrops</i> Illiger, 1800					X			1	1								X
<i>Antipha</i> n. sp.	X							1	23					X			
<i>Clytra nigrocineta</i> Lacordaire, 1848		X						3	1	4							X
<i>C. novempunctata</i> Olivier, 1808			X					1	4	1							X
<i>Smaragdina viridana</i> Lacordaire, 1848		X						4	4	4		5					X
<i>S. limbata</i> Steven, 1806			X					7	7	3				X	X		
<i>S. tibialis hellenica</i> (Marseul, 1868)			X					3						X	X		
<i>S. xanthapsis</i> (Germar, 1824)			X								1			X			
<i>S. cyanea</i> (Fabricius, 1775)			X								1			X			
<i>Coptocephala unifasciata destitui</i> (Fairmaire, 1884)	X				X			3	13	15	10						X
SUBFAMILY CRYPTOCEPHALINAE																	
<i>Cyptocephalus dahdah</i> Marseul, 1868	X						19	5	14	44	5	1					X
<i>C. peyroni</i> Marseul, 1875	X						3	4	2		1			X			
<i>C. crassus</i> Olivier, 1791			X					2									X

continued

APPENDIX—continued

Species	global			Distribution							local			Host spectrum			
	L	EM	A	M	P	H	SF1	SF2	SF3	B	NF5	NF6	NF7	Mp	Op	Pp	
<i>C. bidorsalis</i> Marseul, 1875	X						3		4	3				X			
<i>C. egericki</i> Tappes, 1884		X					2				2		7	X			
<i>Pachybrachis glycyrrhizae</i> Olivier, 1808	X							1	5	6				X			
<i>P. abessinicus</i> Pic, 1913	X									10				X			
<i>P. scripticollis</i> Faldermann, 1837							1	3	4		2	5	4	X			
<i>P. jordanicus</i> Lopatin, 1984	X																
SUBFAMILY EUMOLPINAE																	
<i>Pachnephorus villosus</i> Dufschmid, 1825				X			1		4	6					?		
<i>Macrocoma brumipes</i> Olivier, 1808				X											X		
SUBFAMILY CRYSEMELINAE																	
<i>Chysolina blanchei</i> Fairmaire, 1865	X				X			3				1	2		X		
<i>Ch. polita</i> (Linné, 1758)				X			1		1	2					X		
<i>Ch. gypsophitae</i> (Kuster, 1847)				X			1		1	2					X		
<i>Ch. chalcites</i> Germar, 1824				X					1	2					X		
<i>Ch. palmyrensis</i> Bechyňě, 1955	X						3	1	1	1	1				X		
<i>Ch. schilbergi</i> Menétries, 1836									1	8				X			
<i>Gastrophysa polygami</i> Linné, 1758	X					X			1	1					X		
<i>Gonioctena fomicata</i> ab. <i>piceus</i> Weise, 1884	X										1				X		
<i>Cyrtanastes libanensis</i> Berti & Daccordi, 1974	X							7		1					X		
<i>Entomostelis berytensis</i> Reiche & Saulcy, 1857	X								1	1					X		
SUBFAMILY GALERICINAE																	
<i>Galeruca spectabilis orientalis</i> Oscol, 1844				X				3		3					X		
<i>Diorhabda persica</i> Faldermann, 1837				X					1						?		
<i>Aulacophora foenicollis</i> Lucas, 1849				X				2						X			
<i>Exosoma thoracica</i> Redtenbacher, 1825	X							s	27	17	2		2		X		
<i>Marsaultia dilativentris</i> Reiche & Saulcy, 1857	X						3		10	4	2	1	3		X		
<i>Calomicrus lividus</i> Joannis, 1866	X							9		4	2	1	3		?		
SUBFAMILY ALTIQINAE																	
<i>Phyllotreta corrugata</i> Reiche & Saulcy, 1857				X		X	3	3	26	57		2		X			
<i>P. cruciferae</i> (Goetze, 1777)				X				1	1	2				X			
<i>P. fallaciosa</i> Heikertinger, 1941				X				2	2	6				X			
<i>P. lateritella</i> Kutschera, 1869				X				1	1	6				X			

continued

APPENDIX - continued

Species	Distribution										Host spectrum					
	L	EM	A	M	P	H	SF1	SF2	SF3	local B	NF5	NF6	NF7	Mp	Op	Pp
<i>Longitarsus aeneus</i> Kutschera, 1862				X			5	28	133	25	2	3			X	
<i>L. albivens</i> (Foundras, 1860)			X				1	1		1					X	
<i>L. dabernardii</i> Leonardi, 1979	X							6	5	1	2			X		
<i>L. lycopi</i> (Foundras, 1860)				X						5				X		
<i>L. nigrofasciatus</i> (Goeze, 1775)				X								2		X		
<i>L. allotrophus</i> Furth, 1979	X							1	6	4				X		
<i>L. anchusae</i> (Paykull, 1799)				X				2	3	4				X		
<i>L. emarginatus</i> Weise, 1893	X										Recorded by D. Furth (TAU)			X		
<i>L. fuscovenetus</i> Redtenbacher, 1849					X				2	2	1		2	X		
<i>L. lateripunctatus</i> Rosenhauer, 1856				X								1		X		
<i>L. limnaii</i> (Dufschmidt, 1825)				X					3	1	1	1	1	X		
<i>L. nanus</i> (Foundras, 1860)					X									X		
<i>L. obliteratus</i> Rosenhauer, 1856					X									X		
<i>L. parvulus</i> (Paykull, 1799)					X									X		
<i>L. pellicidus</i> (Foundras, 1860)					X		1		3	1	5	1		X		
<i>L. rectilineatus</i> (Foundras, 1860)				X			3		2	8			1	X		
<i>L. strangulatus</i> (Foundras, 1860)				X						4				X		
<i>L. tabidus</i> (Fabricius, 1775)				X				1						X		
<i>L. saturatus</i> (Matsham, 1802)				X										X		
<i>L. truncatellus</i> Weise, 1893	X						6		1	2	1			X		
<i>L. angusta</i> (Allard, 1863)									2	1	2	5		X		
<i>Aphthona kamtzei</i> Roubal, 1932		X												X		
<i>A. lutescens</i> (Gyllenhal, 1808)				X										X		
<i>A. bonvouloiri</i> Allard, 1859				X				1	3	1				X		
<i>Alicia bicarinata</i> (Kutschera, 1864)				X										X		
<i>Psylliodes chrysocephala</i> (Linné, 1758)				X										X		
<i>P. macrida</i> (Illiger, 1807)				X			2		1	1	3	1		X		
<i>P. drusei</i> Furth, 1983				X										X		
<i>P. cuprea</i> (Koch, 1803)	X						1	1	10	3	1			X		
<i>P. hyoscyami</i> (Linné, 1758)				X			2	1	6	8				X		
<i>Chaetociema tibialis</i> (Illiger, 1807)				X					4	4				X		
<i>Ch. major</i> Jacqueline Duval, 1852				X						12				X		

continued

APPENDIX—continued

Species	L			global			Distribution							Host spectrum			
	L	EM	A	A	M	P	H	SF1	SF2	SF3	local B	NF5	NF6	NF7	Mp	Op	Pp
<i>Hermacophaga nigricollis</i> (Lucas, 1849)				X				1	1	4	4		2		X		X
<i>Ochnosis ventralis</i> (Illiger, 1807)				X				1		3	1				X		X
<i>Orestia brulerieri</i> Allard, 1859	X			X				4	1	1	1	1			X		X
<i>Podagriscia fuscicornis</i> (Linné, 1766)				X				12	25	91	260	2	3	18	X		X
<i>P. matuae sarawana</i> Reiche & Saulcy, 1858				X													
SUBFAMILY HISPIINAE																	
<i>Diadotropa testacea</i> (Linné, 1767)				X							5	17	48	11	X		X
SUBFAMILY CASSIDINAE																	
<i>Hypocassida subferuginea</i> Schrank, 1776				X				1							X		X
<i>Cassida palaestina</i> Reiche & Saulcy, 1858				X					2	4	4			2			X
<i>C. pellegrini</i> (Marseul, 1868)											2						X
Total	16	13	1	38	19	3		81	132	439	612	77	85	67	41	27	12