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Altitudinal effects in assemblages of Drosophilidae (Diptera) in the Ticino, Switzerland

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In the valley of the Ticino river on the southern slope of the Swiss Alps, Drosophilidae were collected at 10 localities along an altitudinal range of 1350 m (Fig. 1). Samples were taken in the morning and evening at most localities, from the inside of forests near their edge, as well as a few meters outside the forest in the adjoining open habitat. Each sample represents a particular species assemblage, differing from others by number and identity of species as well as by their frequency and proportion. Effects of altitude, daytime and habitat were distinguished.

Keywords: Drosophilidae, faunal records, altitude, habitat, assemblage.

INTRODUCTION

Previous samples of *Drosophila subobscura* COLLIN taken in the Ticino valley for a study of gene arrangement frequencies (BORAI *et al.*, submitted), provided additional drosophilid species. In the present report the complete faunistic records are presented. They add basic information to the paper mentioned above and contribute to the general knowledge of Swiss drosophilids. In particular, species proportions were screened for effects of altitude, daytime and habitat.

METHODS

Flies were netted at 8 localities on the bottom of the valley along the Ticino river (Fig. 1), covering an altitudinal range of 1350 m and a horizontal distance of 65 km. Two more samples were taken from a slope (Ravatoi and Angone) at altitudes corresponding to those of the uppermost localities on the valley bottom. Whereas altitudinal effects on the valley bottom might be blurred by horizontal distance, we expect that they are less distorted on a slope. To assess the influence of the alps as a barrier to diffusion, a locality (Göschenen) north of the alpine divide was included in the study.

At each locality, baits were exposed in a forest near its edge, and other baits outside the forest in the adjoining open habitat, which was mostly grassland. The bait consisted of fermenting banana exposed on open plates put on the ground. The number of plates per locality and habitat ranged between 10 and 40 according to the need. The forest is characterized by deciduous trees in the lower part of the valley. Conifers increase in numbers with increasing altitude. The composition of the local plant community including forest type depends on climatic factors such as the length of the vegetation period and the mean temperature during this period. In turn, these climatic factors depend on altitude (Fig. 2; data from SCHREIBER *et al.* 1977). Both vegetation period and temperature are negatively correlated with altitude ($p < 0.001$).

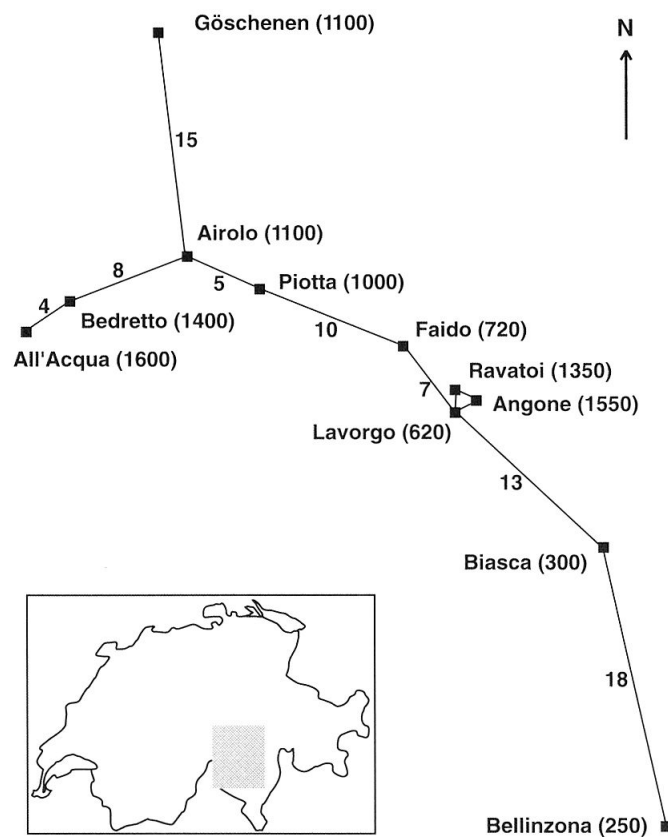


Fig. 1. The sampled localities, with altitude (m) in parentheses and horizontal distances (km). Göschenen is north of the alpine ridge. At bottom left: study area in Switzerland.

During the collecting period (August 11 to 31, 1981) the weather was fair and stable most of the time. Collections were done by two independent groups of collectors. Part of the variation in the records may thus be attributed to unequal collecting strategy of the two groups.

To group species objectively, the ecological overlap between any two species was computed, using the index τ (SCHATZMANN, 1990). On the basis of these values, the species were clustered by a Multidimensional Scaling method (KYSTPLUS program of the PSYCHLIB package). The same clustering method was applied for grouping localities, based in this case on Simple Matching coefficients. For analyzing frequency tables, the program 4F of the BMD package was used. In it, the frequencies are compared to a log-linear model containing effects of selected environmental factors as well as their second order interactions. The partial association option yields a partitioning of the likelihood ratio test statistic (Tab. 2), similar to an analysis of variance.

RESULTS

General

Tab. 1 contains the frequency (number of flies) of each species at each locality. The total number of species, 34, is high, assumedly because of a large variety of environments which was involved. The record includes some species which

Tab. 1. Frequencies (number of flies) of all species recorded. *Drosophila* species are arranged as with BURLA & BÄCHLI (1991). In the genus *Drosophila*, the following groups are made: group I, *obscura* group species; group II, mycophagous species; group III, domestic species; group IV, remaining species. Other genera: Chym., *Chymomyza*; Scapt., *Scaptomyza*; Leuc., *Leucophenga*; *Amiota*. Names of localities are abbreviated from Fig. 1. The first 8 localities, from the floor of the main valley, are ordered by increasing altitude. The next two are on a slope. The last one is north of the alpine divide.

Species	Locality		Bel	Bia	Lav	Fai	Pio	Air	Bed	All	Rav	Ang	Gös	Total
	Code	Group	250	300	620	720	1000	1100	1400	1600	1350	1550	1100	
alpina	AL	I	0	0	1	0	0	1	0	0	52	89	3	146
ambigua	AM	I	1	0	1	0	0	1	0	1	0	2	0	6
bifasciata	BI	I	12	52	41	23	6	1	0	1	0	0	0	136
helvetica	HE	I	2654	92	48	15	0	0	0	0	0	1	0	2810
obscura	OB	I	279	32	206	1314	161	16	23	8	194	228	2	2463
subobscura	SO	I	545	302	1318	2011	212	55	183	104	47	361	71	5209
subsilvestris		I	0	0	0	2	0	0	0	0	0	0	1	3
tristis		I	1	0	7	2	1	0	0	0	0	0	0	11
kuntzei	KU	II	1900	39	84	239	0	0	0	0	1	0	0	2263
limbata		II	2	0	1	1	0	0	0	0	0	0	0	4
phalerata	PH	II	376	31	189	2566	105	3	16	0	32	10	1	3329
transversa	TR	II	6	8	50	53	25	6	40	0	7	137	3	335
testacea	TE	II	1360	149	109	1274	17	1	1	0	23	15	2	2951
histrio	HI	II	87	1	15	29	1	0	0	0	6	3	0	142
cameraria		II	0	0	0	1	0	2	3	0	0	0	4	10
confusa		II	0	0	0	1	0	0	0	0	0	0	0	1
melanogaster		III	37	12	26	3	0	0	0	0	0	1	0	79
simulans		III	33	3	3	1	0	0	0	0	0	0	0	40
hydei		III	0	0	1	0	0	0	0	0	0	0	0	1
immigrans	IM	III	853	15	6	422	1	0	0	0	0	0	1	1298
busckii		III	6	0	0	0	0	0	0	0	0	1	0	7
funebri		III	5	1	1	3	0	0	1	0	0	1	1	13
deflexa		IV	1	0	0	0	0	0	0	0	0	0	0	1
rufifrons		IV	2	0	0	0	0	0	0	0	0	0	0	2
littoralis	LT	IV	0	0	0	0	0	1	1	1	0	0	0	3
nigrosparsa	NI	IV	0	0	0	0	0	0	0	1	0	17	0	18
costata		Chym.	0	0	1	0	0	0	0	0	0	0	0	1
graminum	GR	Scapt.	0	0	1	1	0	0	1	1	7	994	0	1005
pallida	PA	Scapt.	7	1	8	10	0	0	3	1	0	29	9	68
maculata		Leuc.	0	0	0	2	0	0	0	0	0	0	0	2
quinquemaculata		Leuc.	0	0	0	2	0	0	0	0	0	0	0	2
alboguttata		Amiota	0	0	4	8	0	1	0	0	1	0	0	14
rufescens		Amiota	0	0	1	0	0	0	0	0	0	0	0	1
semivirgo		Amiota	9	0	2	0	0	0	0	0	0	0	0	11
Species (S)			21	14	24	23	9	11	10	8	10	15	11	34
Total number of flies (T)			8176	738	2124	7983	529	88	272	118	370	1889	98	22385
Diversity (H')			0.79	0.78	0.64	0.73	0.60	0.56	0.48	0.23	0.66	0.63	0.50	0.95
Equitability (E)			0.60	0.68	0.46	0.53	0.63	0.54	0.48	0.28	0.66	0.53	0.48	0.62

usually are rarely netted, such as *Amiota rufescens* LOEW and *Leucophenga quinquemaculata* STROBL.

All species have been previously collected in Switzerland (BÄCHLI & BURLA, 1985). The following were particularly frequent in the Canton of Ticino: *D. helvetica*, *D. kuntzei*, *D. bifasciata*, *D. phalerata*, *D. transversa*, *D. testacea*, *D. histrio*, *L. maculata* and *S. graminum*. We also expected large numbers of *D. alpina*, *D. ambigua*, *D. subobscura* and *D. nigrosparsa* because these are known to be present at higher altitudes (BURLA & BÄCHLI, 1991). Most wild species which are rare in the present record, are known to be rare generally. All Swiss domestic species were present, three of them in moderate numbers at low altitudes.

Since comparisons between localities are hampered by unequal sample sizes, some of the discussion will be based on species proportions instead of frequencies.

Altitudinal effects

Several *Drosophila* species, among them *D. bifasciata*, *D. helvetica*, *D. kuntzei*, *D. melanogaster*, *D. simulans* and *D. funebris*, were frequent, or present, only below 1000 m (Tab. 1). *D. alpina* was frequent at some, but not all, localities at high altitude, but it was also recorded at Lavorgo (at 620 m). It was very frequent at the two localities on the slope. As it easily escapes being netted, unequal skill of collectors may partly explain these results. The only species with strictly montane occurrence was *D. nigrosparsa*. In general, altitude separates lowland species from highland species.

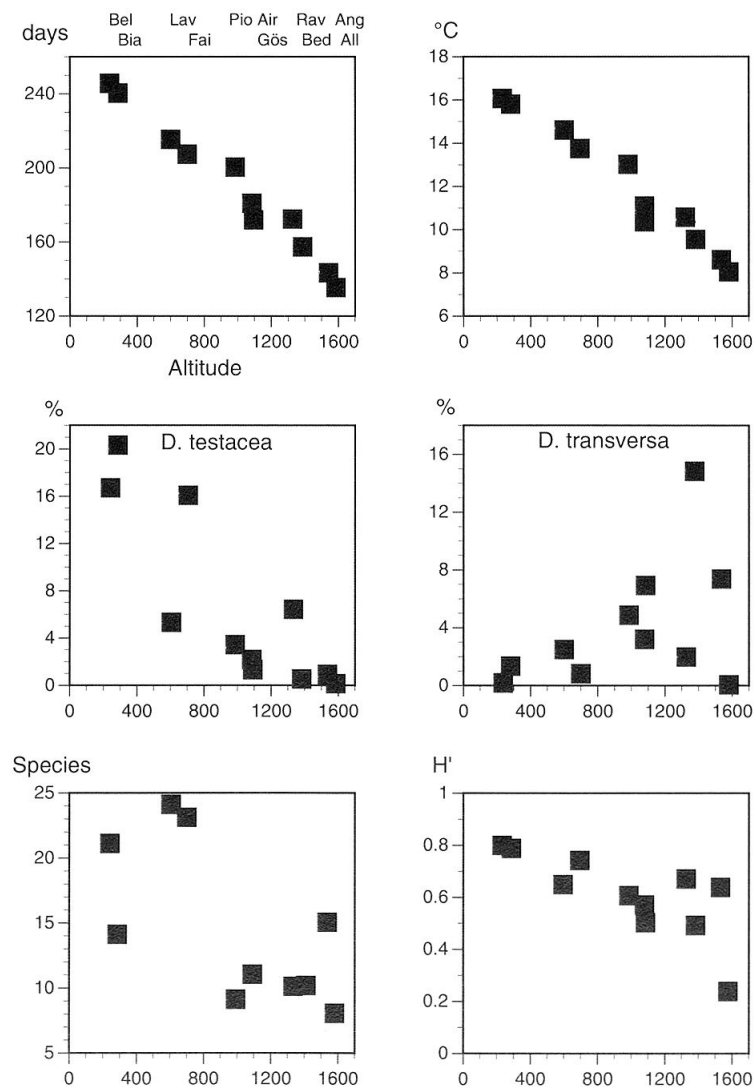


Fig. 2. At top: decrease in the length (in days) of the vegetation period (left) and the mean temperature during the same period (right), with increasing altitude. Middle: proportion of *D. testacea* (left) and *D. transversa* (right) plotted against altitude. Bottom: species number (left) and index of diversity (H' , right) plotted against altitude. The abbreviated locality names are mentioned on top of the plots at left.

Using proportions, the altitudinal pattern of *D. testacea* is shown as a representative example (Fig. 2). Its proportion decreased successively from Bellinzona to Faido. Conversely, the proportion of *D. transversa* (Fig. 2) and *D. subobscura* increased from Bellinzona to higher localities. *S. graminum* was abundant in Angone and rare elsewhere. Most of these results corroborate previous findings (BURLA & BÄCHLI, 1991).

Considering column totals in Tab. 1, the number of species (S), total fly number (T), diversity index (H') and equitability (E) generally decrease with altitude (Fig. 2). Linear regression analysis showed significant altitude effects in S ($p < 0.05$) and H' ($p < 0.01$) but not in T and E. The same effects have been shown by BURLA & BÄCHLI (1991).

The separation of lowland and highland species is demonstrated in Fig. 3, top. The 12 species which were found in 5 or more localities with total numbers of at least 100 were considered. Five species, which were usually found at low altitude, were grouped at the right border. Three species which are mainly collected at high altitude, scatter more widely at the left upper corner. The middle group has a wide altitudinal range. *D. bifasciata* did not fit into any of the groups.

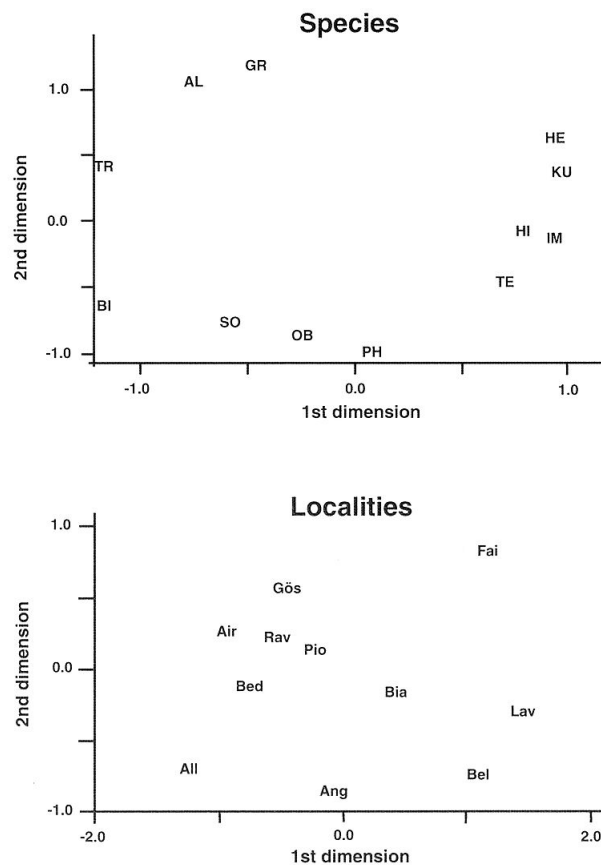


Fig. 3. At top: the 12 most frequent species (codes as in Tab. 1) arranged by Multidimensional Scaling on the base of pairwise ecological overlap as computed by coefficient τ (SCHATZMANN, 1990). Species from high altitude scatter on top at left, low altitude species cluster at the right border, wide-spread species scatter at the bottom. *D. bifasciata* (BI) is isolated at lower left. At bottom: sampled localities (abbreviated from Tab. 1) ordered by species assemblage. The similarity between the proportion of paired species was computed by the Simple Matching Coefficient and arranged by Multidimensional Scaling. Five localities of high altitude cluster on top at left while two others (All'Acqua and Angone) are separated. The four low altitude localities scatter at right.

If altitude strongly determines presence and abundance of species, records from Angone and Ravatoi, which are on a slope above Lavorgo, should equal those from valley localities of comparable altitude. This may be checked in Fig. 3, bottom. The procedure separates low altitude localities (on the right) from high altitude ones (on the left). However, there remain inconsistencies. Piotta (at 1000 m) is too narrowly grouped with alpine localities, while All'Acqua (at 1600 m) is removed from them. Also, whereas Ravatoi (at 1350 m) merges into the group of alpine localities, Angone (at 1550 m) is removed to the bottom of the plot. Apparently, altitude has a strong effect on the composition of the assemblage of species at some localities but not at others. Localities on slopes might be colonized by flies diffusing uphill from the valley bottom, but conditions of the local habitats might have a stronger effect. There is no evidence for an effect of horizontal distance. Actually we did not expect to observe such an effect. If a new species colonizes a valley of the size of the one studied here, the process certainly takes time to reach all parts of the new area. We assume, however, that all species which we record have been well established in the valley for a long time. The maximal horizontal distance of 65 km in the Ticino Valley may be too small to overcome strong effects of the local habitat.

The record from Göschenen north of the alpine divide is similar to the one from Airolo, which is at the same altitude. Thus, Göschenen is grouped close to the Ticino localities of high altitude (Fig. 3). An exchange by diffusion seems unlikely. A pass of 2112 m altitude involving 15 km of rocky alpine grassland above timberline separates Göschenen from the bottom of the upper Ticino valley. We conclude that the faunistical similarity is caused by similar alpine habitats.

Effects of altitude on frequency of individual species have been demonstrated by BURLA (1951), COOPER & DOBZHANSKY (1956), KANEKO (1969) and BÄCHLI (1977). Usually this pattern, which is often subject to seasonal cycles, has been attributed to environmental changes over the altitudinal gap (PIPKIN, 1952; WAKAHAMA, 1962a, 1962b; KAWANISHI *et al.*, 1975; ICHIJO *et al.*, 1982).

Other environmental conditions

At every locality the original data consisted of frequencies, separated by evening and morning as well as by forest and open habitat. A likelihood ratio test (BMDP4F) separated the effects of localities, daytimes and habitats, including second order interactions. The results from 9 of the most frequent species are summarized in Tab. 2. With the exception of *D. bifasciata*, the effect of the three environmental variables was significant at $p < 0.001$, and so were most of the interactions. In seven species, locality was the strongest factor. It contains differences in altitude which no doubt account for its significance. In four species, daytime had a stronger effect than habitat, and in five species the reverse was true.

To go into more details, the proportion of each species at each locality was considered, separate by daytime and habitat, as shown in the following example (*D. phalerata* in locality Bellinzona):

	proportion	
	evening	morning
forest	2.7	7.6
open habitat	1.5	8.8

Tab. 2. Partitioning of a likelihood ratio test statistic (by BMDP4F). At top: output, here shown for *D. subobscura* as a representative example. At bottom: summary of the result of the procedure, carried out with 9 common species. Codes for species as in Tab. 1. L, locality; D, daytime; H, habitat.

<i>D. subobscura</i> at Bellinzona			
effect	degree of freedom	likelihood ratio Chi-square	probability
H	1	63.5	0.0000
D	1	45.6	0.0000
L	5	3350.8	0.0000
HD	1	21.0	0.0000
HL	5	420.3	0.0000
DL	5	1299.9	0.0000

Summary of results; 9 species			
number of localities	species	rank order of main factors	not significant
6	OB	L > D > H	
6	SO	L > H > D	
4	BI	L > H ≈ D	H, D, HT
4	HE	L > D > H	
4	KU	L > H > D	
6	PH	L > D > H	
6	TR	H > L > D	HL
6	TE	D > L > H	
4	IM	L > H > D	

In each cell of the 2x2 table the proportion (in percent) is obtained by dividing the species' frequency by the sum of frequencies over all species, separate by cell and locality. These proportions (within each 2x2 table) were ranked as follows:

	rank	
	evening	morning
forest	3	2
open habitat	4	1

Then, the species were arbitrarily classified according to their patterns of rank orders (Fig. 4). Generally, at high altitude most species had higher proportions in the evening than in the morning, and higher ones in the forest than in the open habitat. At low altitude the species cannot be easily classified because their pattern of rank orders is less consistent. This partly explains the significant interactions between both daytime and habitat with locality (Tab. 2).

		at high altitude			at low altitude		
		at evening	at morning	irrespective of daytime	at evening	at morning	irrespective of daytime
in forest	in forest	SO LT NI				TE GR	KU
	in open habitat	GR					SO TR
irrespective of habitat	in open habitat	AL BI TR TE PA	AM OB PH HI				

Fig. 4. Classification of species according to rank orders, in habitat and daytime, separately by two altitudinal zones. Codes for species as in Tab. 1.

The procedure demonstrates a consistent pattern within species. While the results strictly apply only to the present records in the Ticino Valley, some correspond to patterns known from previous surveys in Switzerland (BURLA & BÄCHLI, 1991).

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ZUSAMMENFASSUNG

Im Ticino-Tal wurden an 10 Orten über eine Höhendifferenz von 1350 m Drosophiliden gesammelt, im Wald nahe dem Rand und auf der benachbarten, offenen Wiese, morgens und abends. An jedem Ort ergaben sich Besonderheiten nach Vorkommen von Arten und deren Häufigkeit. Der Höhenlage, dem Biotop und der Tageszeit konnten Effekte zugeschrieben werden.

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