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A long-term study of a Drosophilidae (Diptera) population

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Collectings of drosophilid flies were made during the years 1986 to 2000 in a woodland area on Hönggerberg (Zürich) and during the years 1987 to 2000 in Dietikon ZH. The faunal drosophilid composition is analyzed, in particular with regard to a coppice with standards experiment, characterized by almost fully cutting a woodland area and letting it regenerate without human manipulation. With increasing regeneration of the wood, the drosophilid composition changes as well, building an almost stable community within about five years. At the beginning of this process, the frugivorous species almost disappear and are partially replaced by fungivorous ones within the next few years.

Keywords. Drosophilidae, ecology, coppice with standards, faunal composition, community regeneration, climax.

INTRODUCTION

Coppice with standards, i.e. coppice with a few large trees, was the traditional silvicultural system in the broadleaf forests in central Switzerland (and many other European countries) until the turn of the 20th century (e.g. Tubbs 1964; Schütz 1993; Evans 1997; Bürgi 1999; Lameire *et al.* 2000; Snakkers *et al.* 2000; Vanck & Spiecker 2004; Rotach 2005; Richard & Chevalier 2006). Every year, a stripe of the forest area was fully cut except for a few large trees. In every following year, an adjoining stripe was cut in the same way, leaving the cut areas unchanged to regenerate. A certain area was managed in this way within about 20 years, before the first stripe was cut again.

The forest authorities of the city of Zürich, as owner of a large forest area on top of the Hönggerberg mountain in the northwestern part of Zürich, decided to start a research experiment, in cooperation with the Chair of Silviculture, ETH Zürich, with the aim of demonstrating the dynamics of the system and getting results about the regeneration of the forest area and the related effects on the faunal composition. It was supposed that the strongly changed forest structures and light conditions could have a positive effect on the local biodiversity, particularly on some endangered plant and animal species, as shown by several studies (e.g. Barkham 1980; Richard & Chevalier 2006).

During the 20th century, almost all coppices with standards were slowly transformed into stands operated by modern methods. On the Hönggerberg, however, the forest has still many aspects of the ancient coppice with standards type. It was, therefore, selected as an experimental area, in which the ancient methods could be reestablished. To get results within a reasonable time, the traditional method – allowing some 20 years for full regeneration – was altered into a seven years cycle with replications. Several accompanying studies for changes in floral and faunal groups were undertaken, e.g. land snails, ground beetles, amphibians, birds, and Drosophilidae. Related results of such regeneration studies have already been published (e.g. Barkham 1980; Fonti *et al.* 2000; Guilley *et al.* 2004; Kowalski *et al.* 2004; Richard & Chevalier 2006).

Long-term studies of faunal compositions have been made for various animal groups (see e.g. Wagner & Schmidt 2004). Also, a few such studies on the distribution of drosophilids have been made, either by annual repetition of collectings (e.g. Brncic *et al.* 1985, during three years, or Benado & Brncic, 1994, during seven years) or by samples collected widely separated in time (e.g. Argemí *et al.* 1999, 2003). The majority of such studies, however, have been made for the analysis of seasonal changes, particularly for the study of characteristics of natural populations (e.g. Dobzhansky & Epling 1944; Epling *et al.* 1953; Dobzhansky 1956; Paik 1957; Burla 1961; Watabe *et al.* 1980; Beppu *et al.* 1996). Our study does not only give some long-term data about the population composition but also on the population change during the period of forest regeneration. In particular, the following aspects were addressed:

- Is there any trend in the drosophilid fauna after the cut?
- Does this trend lead to a permanent drosophilid community (climax)?
- Does this trend have a particular influence on the presence and abundance of certain species?

MATERIAL AND METHODS

Study areas

A part of the forest area on the Hönggerberg, about 520 m a.s.l., is shown in Fig. 1. The coppice with standards sections are marked with the letters A to C. The experimental study was started in 1984/1985 by cutting the trees in the sections A and B. In 1991, the trees in the area C were cut. For our study, the area C was used as a control collection until the second cut, but collecting was continued afterwards. An additional control collection was made in a rather different, old gallery forest along a small river near Dietikon ZH, 390 m a.s.l., about 10 km west of Zürich.

Collecting

Collecting was started in the areas A to C in 1986, i.e. one year after the first cut. At that time, the vegetation in area C was an unchanged, traditional mixed forest, whereas in areas A and B, except for a few large standards, almost no vegetation existed. In the following years, the vegetation regenerated, at the beginning with *Rubus* sp. in thick stands.

In each of the areas A to C, 10 positions were selected for placing open baits on the ground, containing mashed, fermenting bananas. During five days, flies were collected every evening during the main activity time of the drosophilids by net sweeping. Three collectings were made at intervals of 15 to 20 minutes, in the meantime allowing additional flies to be attracted by the baits. The arrangement of collecting places was maintained during all years, as far as the vegetation allowed it.

In Dietikon, around 10 baits were placed in the same manner, but this refer-

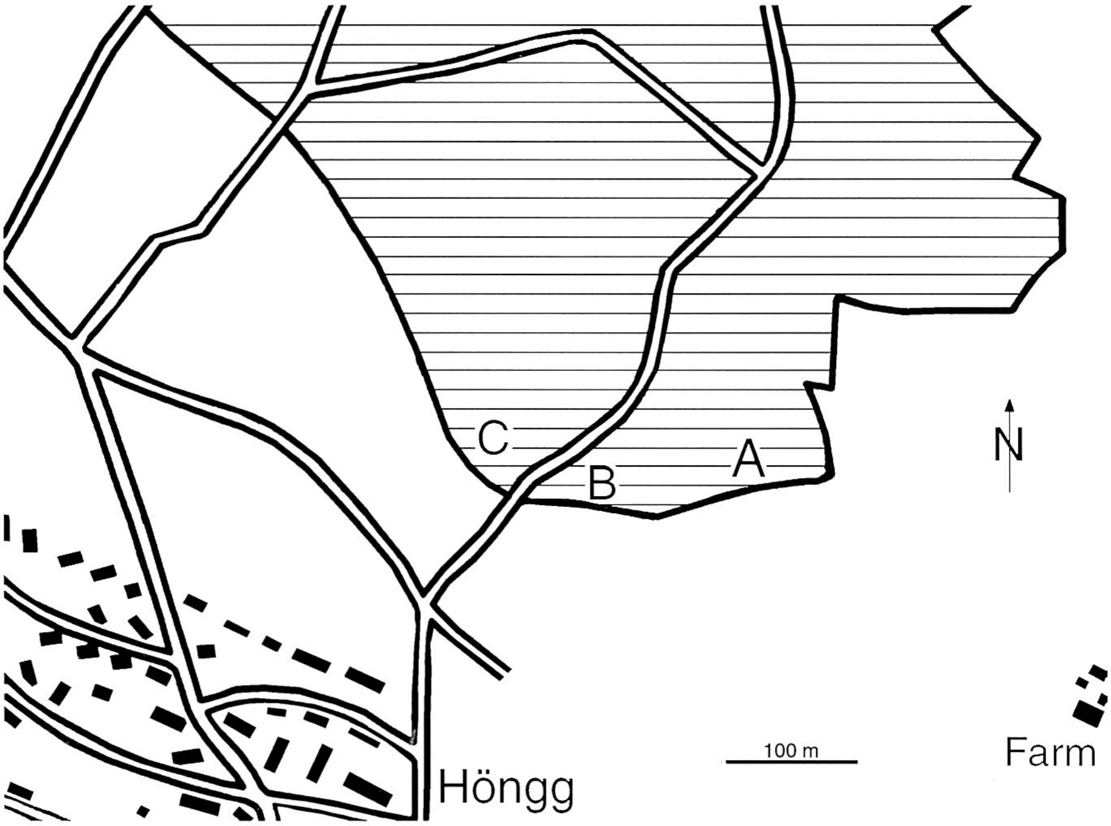

Fig. 1. Study area on the Hönggerberg mountain, Zürich. A, B, C = collecting areas.

ence collection was made only twice every evening. Collectings in Dietikon started in 1987, i.e. one year after the collectings in Hönggerberg.

From 1986 to 1992 two collection series per year were made, a summer collection in July and an autumn collection in September; from 1993 to 2000 collections were made in July (late June in 1999, early August in 1997) only. All samples were pooled, forming a sampling unit per season, year and area.

Descriptive analysis

For the evaluation of the biodiversity, we used the Shannon/Weaver index

$$H' = -\sum (p_i) \cdot \log (p_i)$$

where p_i is the relative contribution of species i to the sample. The Simpson Index

$$D = 1 - \sum (p_i^2)$$

was used for partitioning the diversity into components (Lande 1996; Fournier & Loreau 2001). The indices H' and D were highly correlated. In addition, we used the equitability index

$$E = H'/\log(S)$$

where S is the number of species per sample (Pielou 1972, 1974; Bächli 1979). Also, the exponential form,

$$EXP(H')$$

was used, (as suggested by Peet 1974), interpreted as the effective number of species in the sample.

Statistical long-term analysis

The aim of the statistical analysis was to answer the main question: How are the changes of the habitats reflected by the drosophilid fauna? In particular, the following questions have been addressed:

- Is there any general tendency after the cut?
- Are the areas A and B similar and both rather different from C?
- Is there any similarity between the area C after the cut in 1991 with the areas A and B after the cut in 1984/1985?
- Do species react differently?

Experimentally there were collections available from 1986 until 2000 from sites A, B and C from Hönggerberg, whereas wood had been cut at sites A and B before 1986, and at site C between collections 1991 and 1992.

Before we performed any relevant analysis, we decided to concentrate on forest species of the Hönggerberg area, to omit rare species, and to use only collections of comparable seasons. We therefore included only species with more than 100 flies in the summer collections, but excluded the domestic species *D. immigrans* Sturtevant, the ubiquist *S. pallida* (Zetterstedt) as well as *C. amoena* (Loew), a species not present in Switzerland before 1988. Finally, 12 relevant species were included. And we only used the summer collections in July, including 1997 and 1999, for which collections of early August and late June, respectively, were available.

In order to answer the questions above, we wanted to visualize the development of the drosophilid fauna at the three areas A, B and C over the years with statistical methods. Therefore, the table with the raw data, showing the number of specimens of the different species caught in the three experimental areas of the Hönggerberg from 1986 until 2000, somehow had to be projected to 3 x 15 points placed in the plane, reflecting the faunal compositions at the 3 areas over the 15 years.

With principal component analysis (PCA), the numbers of specimens caught in each experimental area should be reduced to a few dimensions that contribute most to the differences between the faunas. For this analysis there were several problems to overcome.

Numbers of drosophilids generally show aggregated distributions. This may be due to common breeding sites, common attractors etc. As PCA theory is based on normal distributions, as a first transformation we took the square roots of the raw numbers. Ideal, independent counts would have a Poisson distribution, which for not too small numbers is close to normal. The Poisson distribution is characterized by a variance to mean ratio of 1. Corresponding collections in experimental areas A and B can be seen as independent samples under the same conditions. We could calculate that in order to get a mean variance to mean ratio of 1 within all pairs of A and B per species, season and year, it would have been necessary to raise the raw numbers to the power 0.53. We applied the very similar but more common square root transformation, which corresponds to an exponentiation with 0.5.

The total number of specimens collected by net sweeping in a certain place at a certain time is influenced by factors like wind, temperature, light conditions, obstacles etc. In order to eliminate such effects, in a second transformation, for each sampling unit we divided the number of specimens of each species by the total number of specimens of all species.

If specimens in a collection stem from a rare species they generally are of bigger relevance than if they belong to a common species. To account for that we divided in a third transformation the number of specimens of each species and sampling unit by the total number of this species over all sampling units. This third transformation, however, is already performed by the PCA program automatically.

All transformations together can be formulated as

$$R_{ij} = \sqrt{(N_{ij})}$$

$$S_{ij} = R_{ij} / R_{.j}$$

$$T_{ij} = S_{ij} / S_{i.}$$

where i = species, j = sampling unit, N_{ij} = number of specimens of i caught at j, $R_{.j}$ = total of all R_{ij} over all i, $S_{i.}$ = total of all S_{ij} over all $_j$.

We are aware that the sequence of the transformations shown is not mandatory. In fact the different disturbing effects noted above may partially act simultaneously. In addition, the mechanisms may differ from species to species. But we think that the three transformations shown were important for a meaningful PCA.

The PCA was then performed on the correlation matrix of the T_{ij}-values with SAS 6.1. The PCA-program was only told the species and the ID of the sampling unit, but not the experimental area and not the year. Area and year were added back only afterwards to plot the sampling units by area and year against the two main components. To the resulting data we fit a general linear model with procedure GLM of SAS, with PC1 and PC2 as dependent variables; independent variables were: sampling area; whether the collection was before or after the cut; Z = the inverse of the number of years after the cut; Z^2; Z^3; and the interaction between sampling area and Z. For the years before the cut in area C, Z was set to 0.01, to express a long time. The information of PC1 and PC2 mapped by the model (R^2) was 84 % and 79 %, respectively (Fig. 2).

In a second plot, the eigenvectors, i.e. correlations between the original variables (the species) and the first two principal components (PC) are shown (Linder & Berchtold 1982). This allows for interpreting the meaning of the main components (Fig. 3).

In order to get an overview over the general change of the three drosophilid faunas during the experiment, the estimated PC1/PC2 pairs from Fig. 2 then were plotted in the PC1 by PC2 plane and connected over the years by a smoothing function (Fig. 4).

Tab. 1. List of drosophilid species collected during this study. For each locality, the total number of flies is given, pooled over the respective collection period. In addition, some diversity indices are mentioned.

Species	Hönggerberg	Dietikon	Total
Amiota albilabris (Roth, 1860)		2	2
Amiota alboguttata (Wahlberg, 1839)		2	2
Amiota basdeni d'Assis Fonseca, 1965	20	10	30
Amiota flavopruinosa Duda, 1934		1	1
Chymomyza amoena (Loew, 1862)	218	23	241
Chymomyza caudatula Oldenberg, 1914	1		1
Chymomyza fuscimana (Zetterstedt, 1838)		3	3
Drosophila ambigua Pomini, 1940	15		15
Drosophila busckii Coquillett, 1901	9	29	38
Drosophila funebris (Fabricius, 1787)	7	12	19
Drosophila helvetica Burla, 1948	46141	15847	61988
Drosophila histrio Meigen, 1830	622	141	763
Drosophila hydei Sturtevant, 1921	14	126	140
Drosophila immigrans Sturtevant, 1921	3028	7152	10180
Drosophila kuntzei Duda, 1924	3741	5868	9609
Drosophila limbata von Roser, 1840	170	531	701
Drosophila littoralis Meigen, 1830	2	111	113
Drosophila melanogaster Meigen, 1830	141	224	365
Drosophila obscura Fallén, 1823	6398	2850	9248
Drosophila phalerata Meigen, 1830	6872	7696	14568
Drosophila repleta Wollaston, 1858	95	1	96
Drosophila simulans Sturtevant, 1919	268	320	588
Drosophila subobscura Collin, 1936	30801	13246	44047
Drosophila subsilvestris Hardy & Kaneshiro, 1968	1217	107	1324
Drosophila testacea von Roser, 1840	7675	4228	11903
Drosophila transversa Fallén, 1823	144	11	155
Drosophila tristis Fallén, 1823	153	93	246
Hirtodrosophila cameraria (Haliday, 1833)	176	1	177
Hirtodrosophila confusa Staeger, 1844	133	152	285
Leucophenga hungarica Papp, 2000	2		2
Leucophenga maculata (Dufour, 1839)	8	3	11
Lordiphosa andalusiaca (Strobl, 1906)		1	1
Lordiphosa fenestrarum (Fallén, 1823)	10	14	24
Lordiphosa nigricolor (Strobl, 1898)	3	5	8
Microdrosophila congesta (Zetterstedt, 1847)		1	1
Phortica semivirgo (Máca, 1977)	39	34	73
Phortica variegata (Fallén, 1823)	33	22	55
Scaptodrosophila deflexa (Duda, 1924)	467	345	812
Scaptodrosophila rufifrons (Loew, 1873)	15	18	33
Scaptomyza flava (Fallén, 1823)	2	4	6
Scaptomyza graminum (Fallén, 1823)	100	29	129
Scaptomyza pallida (Zetterstedt, 1847)	529	218	747
Stegana coleoptrata (Scopoli, 1763)	12	5	17
Stegana longifibula Takada, 1968	8		8
Stegana nigrithorax Strobl, 1898	9	4	13
Stegana similis Laštovka & Máca, 1982	5	4	9
Total specimens	109301	59494	168795
Number of Species	40	42	46
Diversity H'	1.703	2.018	1.859
EXP (H')	5.490	7.527	6.419
Simpson's D	0.728	0.831	0.775
Equitability	0.465	0.540	0.488

RESULTS AND DISCUSSION

Overview

As shown in Tab. 1, at each locality more than 40 species were recorded, representing about two thirds of the species found in Switzerland (Bächli 1998). Among them are six species known as domestic, e.g. *Drosophila busckii*, *D. melanogaster*, etc.; except *D. immigrans*, all of them were relatively rare, as can be expected in a predominantly natural habitat.

One of the dominant species was *D. subobscura*, as can be expected according to almost all Swiss collections (Bächli & Burla 1985; Burla & Bächli 1991), but elsewhere as well (e.g. Argemí *et al.* 1999). However, even more flies were collected of *D. helvetica*, a species rarely occurring in such large numbers (but see Bächli *et al.* 2006). Abundant species were also *D. phalerata*, *D. testacea* and *D. immigrans*, whereas *D. obscura*, usually faunistically associated with *D. subobscura* (Greuter 1963), was distinctly less abundant.

The majority of the recorded species can be expected in collections made using banana baits (Burla & Bächli 1991). Some species, however, are normally not attracted by such baits (see e.g. Argemí *et al.* 1999; less comparable are Brncic *et al.* 1985 and Benado & Brncic 1994) and are found predominantly by net sweeping, in particular among the herbaceous layer and around rotting wood. The species of the following genera belong to this category: *Amiota*, *Chymomyza*, *Lordiphosa*, *Microdrosophila*, *Phortica*, *Scaptodrosophila*, *Stegana*. It is known, however, that such species, sitting on or flying around plants in the vicinity of a bait, are accidentally netted. In addition, some flies obviously visit fresh baits because of their moisture (Bächli & Burla 1985). Records of particularly rare species (Bächli *et al.* 2004) have been made in Dietikon: *Amiota albilabris*, *Amiota flavopruinosa*, *Lordiphosa nigricolor*, *Microdrosophila congesta*; in Hönggerberg: *Leucophenga hungarica* (first record in Switzerland), *Lordiphosa nigricolor*. There are also some obvious differences in the abundances between the Hönggerberg and Dietikon sites: Among the generally rare species, the following were particularly abundant in Hönggerberg: *C. amoena*, *D. ambigua*, *D. histrio*, *D. repleta*, *D. transversa*, and *H. cameraria*, whereas this effect was observed for *D. hydei* and *D. littoralis* in Dietikon. For *D. transversa*, we suppose that this fact is based on an altitudinal effect, for *D. littoralis* it is the vicinity of the river. We did not study the ecological background in detail.

Banana baits are undergoing a typical process of aging during the five days of collecting. The fresh bait, strongly fermenting, is chiefly attractive for frugivorous species. The majority of flies are «dark», i.e. belong to the *obscura* group or other frugivors (Schatzmann 1977). After two or three days, because of the progressive fermentation the smell of acetic acid can be observed and the flies collected are more and more «yellow», i.e. belong to *D. immigrans* and to the fungivorous species, particularly to the *quinaria* group species and to *D. testacea*.

The weighted contribution of the Hönggerberg / Dietikon samples to the total diversity (beta component) is 58 %.

Tab. 2. List of drosophilid species collected at Hönggerberg. For each year, the total number of flies is given, pooled over the three areas A, B and C. In addition, some diversity indices are mentioned.

Year / Species	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
A. basdeni				1	4	1	3				4		2		5
C. amoena			1	4	8	41	9	7	12	50	45	5	31	3	2
C. caudatula		1													
D. ambigua		2	4	2	1	5		1							
D. busckii			1		2		1			1	3			1	
D. funebris					7										
D. helvetica	889	5308	3249	2331	9208	12366	2258	324	2161	3357	3346	219	519	562	44
D. histrio	7	6	16	15	14	26	182	1	138	138	25	6	7	35	6
D. hydei					6	2		1	2	2	1				
D. immigrans	442	188	304	212	268	127	162	11	222	181	192	156	184	362	17
D. kuntzei	78	101	165	98	186	561	417	33	218	383	248	174	404	582	93
D. limbata		31	49	37	31	3	4		4	3	1	2	3	2	
D. littoralis		1											1		
D. melanogaster	58	8	8	2	8	24	17	2	8	2	2	2			
D. obscura	477	1139	422	865	605	1562	94	32	129	63	353	84	178	306	89
D. phalerata	231	105	287	60	176	733	1467	91	222	543	367	178	777	1321	314
D. repleta						95									
D. simulans	149	1	17	26	40	20	2		9	3		1			
D. subobscura	2407	4382	1274	5212	2855	3601	1337	656	418	3569	581	495	778	2909	327
D. subsilvestris	53	237	241	283	132	246	7	1	7		4	5			1
D. testacea	105	207	394	194	398	446	500	69	691	1006	1183	267	647	1370	198
D. transversa	34	9	4	1	1	1	11	1		22	36	12	6	5	1
D. tristis	1	13	3	18	25	69	1	2	5		12	2		1	1
H. cameraria	1	2	173												
H. confusa	5	12	11	4	24	9	2	2	9	7	1	18	6	13	10
L. hungarica													2		
L. maculata			1			1			1	2	1	1	1		
L. fenestrarum			1		5	1					2		1		
L. nigricolor					2								1		
P. semivirgo	2	1	1	9	4	9	2				11				
P. variegata	2	5	2		3	4		1			2		2	12	
S. deflexa	9	10	28	48	165	140	13	2	32	1	7	8		2	2
S. rufifrons	6	1	1		1	3	1		2						
S. flava			1						1						
S. graminum		11	16	6	20	35	4		1	1	1	2	3		
S. pallida	5	137	80	60	94	35	4	1	2	10	15	35	37	14	
S. coleoptrata						7	3			1	1				
S. longifibula								1		1	5			1	
S. nigrithorax							1			2			5		1
S. similis						1									4
Totals	4961	11918	6754	9488	14293	20174	6502	1239	4294	9348	6449	1672	3593	7501	1115
Number of Species	20	25	28	22	29	30	25	20	22	23	27	20	22	18	17
Diversity H'	1.682	1.366	1.780	1.383	1.248	1.352	1.744	1.390	1.672	1.516	1.584	2.052	1.958	1.727	1.787
EXP (H')	5.375	3.921	5.929	3.986	3.484	3.866	5.721	4.014	5.321	5.554	4.873	7.782	7.082	5.624	5.969
Simpson's D	0.711	0.656	0.719	0.628	0.542	0.584	0.775	0.641	0.701	0.708	0.680	0.836	0.835	0.770	0.788
Equitability	0.561	0.424	0.534	0.447	0.371	0.398	0.542	0.464	0.541	0.483	0.480	0.685	0.643	0.598	0.631

Hönggerberg

The flies collected in Hönggerberg are summarized in Tab. 2, pooled over all collections per year. We want to mention that the record of *C. amoena* in 1988 is one of the first in Switzerland (Máca & Bächli 1994); it was present during all following years, and relatively large numbers of flies were collected in some years, probably originating from the apple orchards situated around the adjacent farm.

Seen from the totals per year, it is obvious that strong fluctuations from year to year can be observed. Provided that the collecting efforts were comparable during the whole period (i.e. the collector's ability was only lightly reduced by rain, wind, etc. during the sampling hours), we are convinced that changing weather conditions

Tab. 3. List of drosophilid species collected at Dietikon. For each year, the total number of flies is given. In addition, some diversity indices are mentioned.

Year	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
Species														
A. albilabris									2					
A. alboguttata	2													
A. basdeni			2	1		4		1		1		1		
A. flavopruinosa				1										
C. amoena				1	3	7	1	1		1	4	1	3	1
C. fuscimana			3											
D. busckii	1			9	3	9		7						
D. funebris		1		2	3	1				5				
D. helvetica	1951	636	400	3400	5139	1197	31	673	1703	307	171	146	88	5
D. histrio	12	7	5	4	11	5	3	25	21	5	21		22	
D. hydei		3	1	51	25	19		9		4	3	1	10	
D. immigrans	462	409	401	1347	280	1015	32	679	193	84	1099	150	978	23
D. kuntzei	637	418	250	893	869	420	32	205	242	262	588	375	642	35
D. limbata	87	55	34	103	42	41	15	11	22	11	32	24	50	4
D. littoralis	16	4	16	3	21	12	6	10	3	8	2	10		
D. melanogaster	14	9	5	29	56	50	1	27	1	4	23		5	
D. obscura	433	166	279	351	791	70	30	74	56	205	196	41	149	9
D. phalerata	469	423	164	1003	1051	1406	138	246	364	448	622	384	886	92
D. repleta				1										
D. simulans	1	13	41	54	138	9	1	22	8	1	13	4	15	
D. subobscura	958	187	1671	1321	3993	1361	210	158	846	504	333	214	1420	70
D. subsilvestris	40	17	19	9	13		2	4	1	2				
D. testacea	274	346	163	518	409	508	40	355	427	165	248	191	557	27
D. transversa					1	8				1	1			
D. tristis	7	5	3	30	29			2	3	11	3			
H. cameraria									1					
H. confusa	6	9	3	20	1	7	1	60	1		37	3	3	1
L. maculata	1	1											1	
L. andalusiaca				1										
L. fenestrarum	3					1	1	1	3	5				
L. nigricolor			1	1						1	1			1
M. congesta				1										
P. semivirgo	3		1	1	23	3		3						
P. variegata		1	4	2		7	3		1			1		3
S. deflexa	8	78	65	60	66	25	6	11	10	8	4		4	
S. rufifrons		1		14	1	2								
S. flava			3									1		
S. graminum		1	15	4	4	1	2		2					
S. pallida	27	4	32	11	65	9	6	17	26	7	3	3	1	7
S. coleoptrata	1	1			1	2								
S. nigrithorax				3	1									
S. similis				3	1									
Totals	5413	2795	3581	9252	13040	6199	561	2601	3936	2050	3404	1550	4834	278
Number of Species	23	24	25	33	28	27	20	23	22	23	20	17	17	13
Diversity H'	1.920	2.135	1.858	1.927	1.690	1.929	1.939	2.055	1.686	2.001	1.935	1.925	1.82	1.853
EXP (H')	6.819	8.456	6.412	6.870	5.418	6.883	6.955	7.804	5.400	7.397	6.923	6.857	6.169	6.382
Simpson's D	0.801	0.857	0.741	0.797	0.735	0.825	0.781	0.826	0.740	0.835	0.812	0.827	0.807	0.793
Equitability	0.612	0.672	0.577	0.551	0.507	0.585	0.647	0.655	0.546	0.638	0.646	0.680	0.642	0.723

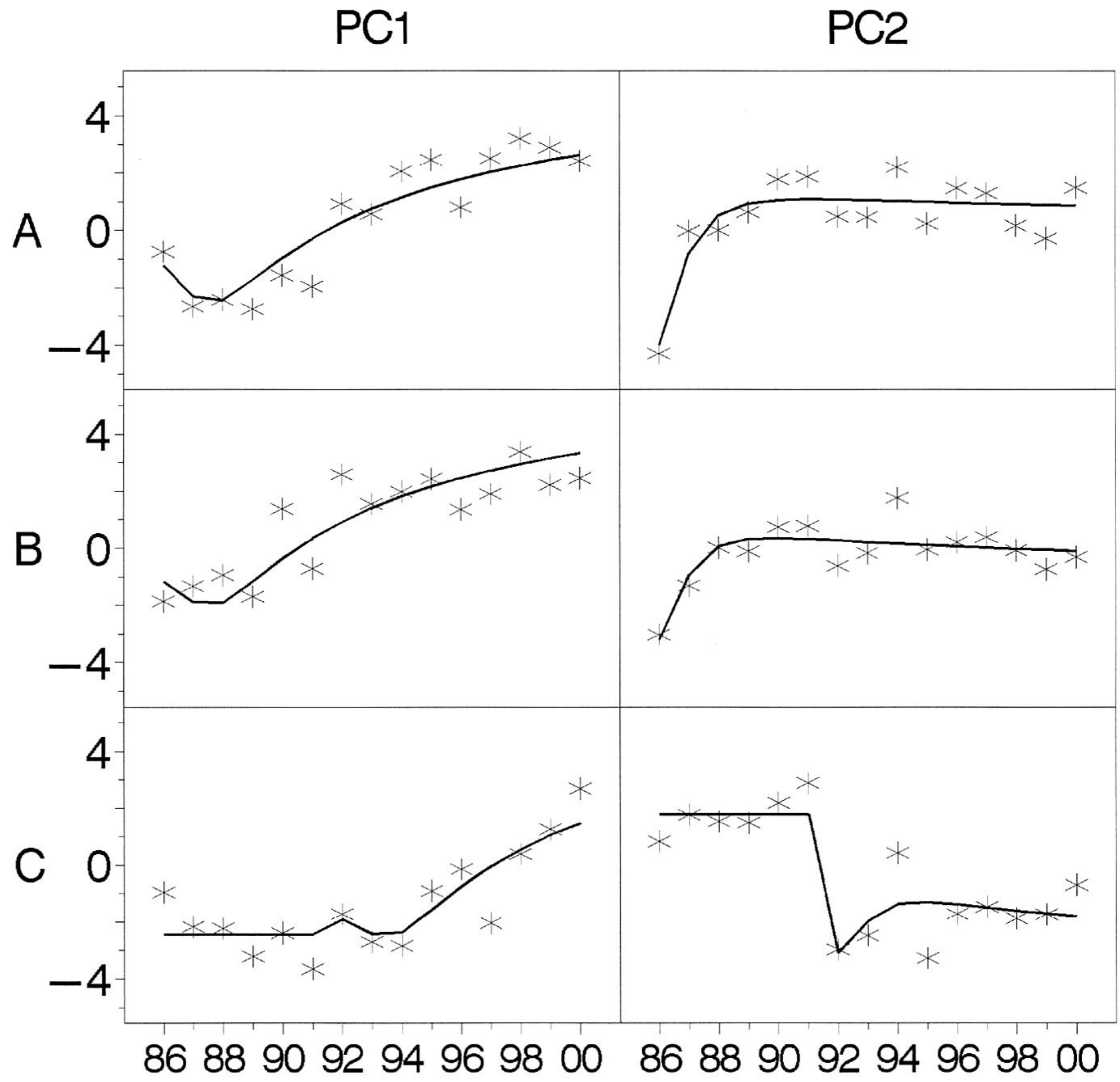

Fig. 2. First two principal components (PC1, PC2) of faunas in areas A, B and C from 1986 to 2000. Stars indicate the original values, curves show the fitted model. In areas A and B wood cut was in 1984/1985, in area C between the collections of 1991 and 1992. Similarity of areas A and B, effect of wood cut, and its delay in C are clearly reflected.

are responsible for this effect. It is not the aim of this study to refer to climatic conditions. We have available the weather conditions during the sampling hours, but do not use them for explaining the fluctuations, in particular because such fluctuations are most probably long-term effects of the conditions during the whole preceding year. Anyway, the weighted contribution of the annual samples to the total diversity (beta component) is about 6 % only.

Dietikon

The flies collected in Dietikon are summarized in Tab. 3, pooled over all collections per year. The collections started one year after the ones in Hönggerberg. Again, *C. amoena* showed up, for the first time in 1990 and in low numbers during almost all following years.

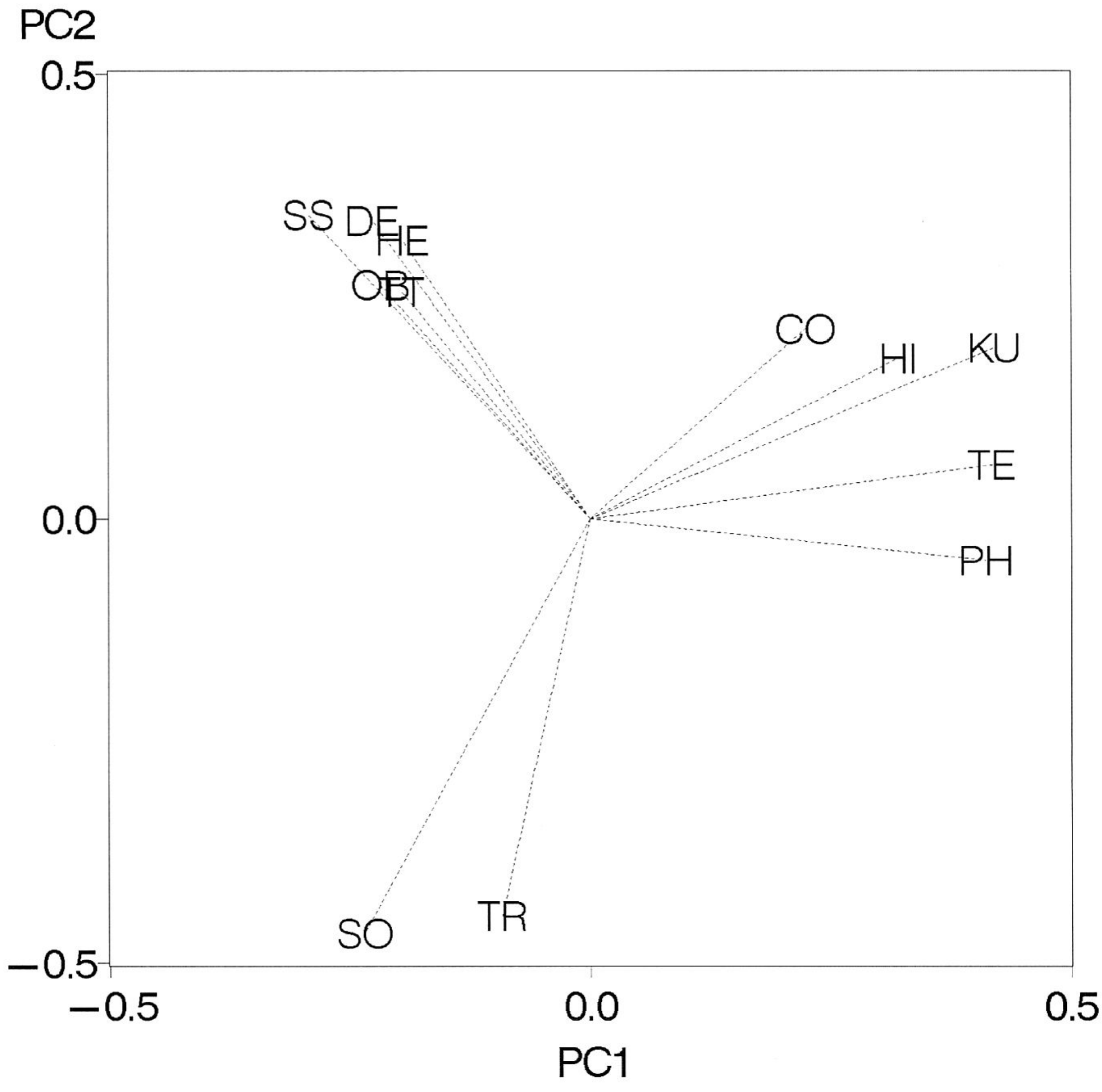

Fig. 3. Plot of the correlations between species and principal components. Species abbreviations are: CO, *H. confusa*; DE, *S. deflexa*; HE, *D. helvetica*; HI, *D. histrio*; KU, *D. kuntzei*; OB, *D. obscura*; PH, *D. phalerata*; SO, *D. subobscura*; SS, *D. subsilvestris*; TE, *D. testacea*; TR, *D. transversa*; TT, *D. tristis*; frugivorous species are placed in the left upper corner, fungivorous species in the right center.

Again, we observed strong annual fluctuations, almost parallel to the ones at the Hönggerberg site. However, the weighted contribution of the annual samples to the total diversity (beta component) is less than 7 %.

Not only the presence of some rare species but also the biodiversity indices, being larger than those in Hönggerberg (Tab. 1), account for Dietikon as a particularly interesting site. Therefore, this collection is very useful as a control. We have to consider, however, that a single-year collection, usually containing some 20 species (see Tab. 2 and Tab. 3), is not much different from similar collections made in Switzerland (Burla & Bächli 1991).

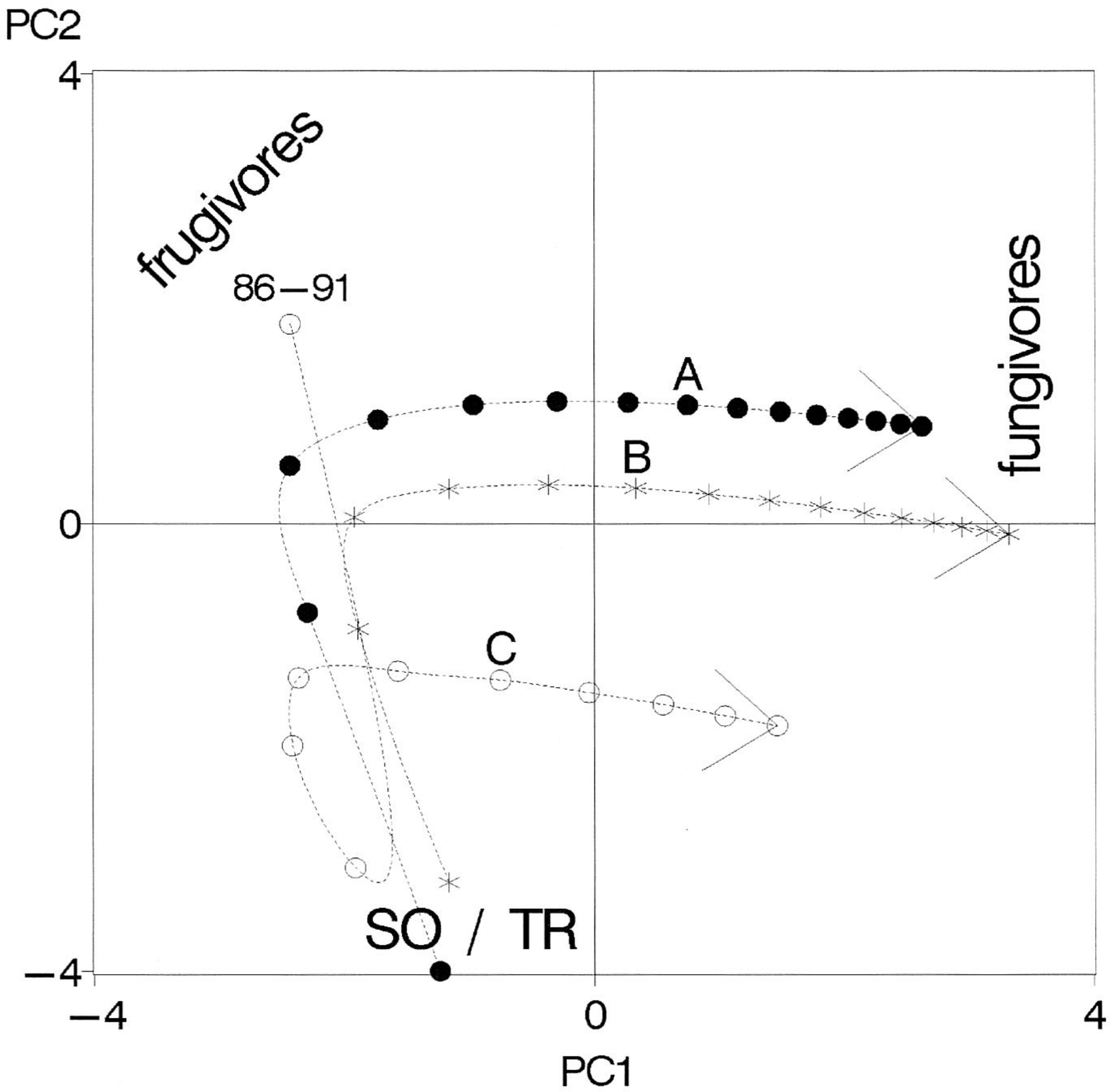

Fig. 4. Changes of drosophilid faunas. Curves connect the estimated 15 PC1/PC2 pairs for each of the areas A, B and C from 1986 to 2000, with 2000 at the tip of the arrows. For area C, the estimates from 1986 to 1991, i.e. before the wood cut, are identical; "frugivores", "fungivores", and "SO / TR" are groups of species as identified in Fig. 3.

Long-term changes

The drosophilid faunas of the Hönggerberg could be projected to two principal components, which contain 38 % and 21 % respectively of the original information, together 59 %. We ignore subsequent components, as they contain only 10 % and less each. The characterization of the yearly faunas of the three experimental areas by the first two components are plotted in Fig. 2. As expected, the repetition areas A and B behave similarly whereas C shows its own pattern. The wood cut between 1991 and 1992 in area C is dramatically reflected by PC2. Parallel deflections in these and several other years, especially in 1994 for PC2 are probably artifacts due to the initially used transformations. However, a general trend after the wood cut appears for all three curves, if curve C is shifted back by six years to correct for the delay in cut.

The inspection of the correlations between species and principal components shows that PC1 represents mainly fungivorous species, whereas PC2 is positively associated with frugivorous species and negatively with *D. subobscura* and *D. transversa* (Fig. 3).

In Fig. 4 the general change of the three summer faunas during the 15 experimental years is summarized. Each of the three curves represents the series of data pairs of the corresponding area A, B or C of Fig. 2, after fitting a model with a constant term for the years before the wood cut and a cubic term after the cut, for each area. Again, it turns out that the courses of the faunas in A and B were similar, which was expected, because A and B experimentally are repetitions.

Collections before the wood cut are not available except for area C from 1986 until 1991. These collections are summarized by the circle labeled «86–91» in Fig. 4, and are characterized by frugivorous species.

The three faunas from the first year after the cut are placed closely together, namely at the bottom of the graph, which is dominated by *D. subobscura* and *D. transversa* (SO/TR). For A and B, this was in 1986, and for C in 1992. Already in Fig. 2 the corresponding faunas show similar values on the main components; however, the collection from 1995 in area C had a similar fauna too, what does not show up in Fig. 4 because of the rougher model.

According to Fig. 4 the portion of frugivorous species generally gets partially reestablished up to the third year after the wood cut. But from the fourth year on, frugivores diminish in favour of fungivores.

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ZUSAMMENFASSUNG

Im Rahmen eines Mittelwald-Projektes wurden von 1986 bis 2000 im Wald des Hönggerbergs ZH und von 1987 bis 2000 in einem Wald bei Dietikon ZH Drosophiliden gesammelt. Die Analyse ergab, dass sich kurz nach dem Fällen der Bäume die Zusammensetzung der Fauna deutlich änderte, wobei die Fruchtfresser- und die Pilzfresser-Arten sich unterschiedlich verhielten. Innert etwa 5 Jahren näherte sich die Zusammensetzung der Fauna dem vorherigen Bestand an Arten und Individuen an, aber mit einer relativen Zunahme von Pilzfressern.

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