Consequences of Succession on Extensively Grazed Grasslands for Central European Butterfly Communities: Rethinking Conservation Practices

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Abstract: *Because of changes in land use, the quantity of extensively grazed or mown calcareous grasslands and their successional stages have drastically declined over the last few decades in Central Europe. Old fallow land has decreased most. It is often afforested or reconverted into extensively cultivated grassland because extensive cultivation is believed to be favorable for diversity and rare species conservation. The relative importance of fallow calcareous grasslands, however, has not been investigated fully and might be much underestimated. To evaluate the relative importance of extensively grazed pastures, early and old fallow land, and young forest, we examined populations of diurnal butterflies from 14 sites in the Swiss Jura Mountains. We used univariate, multivariate, and qualitative methods to compare the successional stages. The first 2–3 years of succession had little influence on the butterfly fauna. Therefore, pastures and early fallow land were treated as a single "early stage." Old fallow land had significantly higher species richness (+32%) and heterogeneity (+65%) and hosted more Red List species (+48%) than the early stage. Young forest was depauperate in butterfly species. Further, cluster analysis and correspondence analysis showed a close resemblance of the sites of the early stage to each other and a clear difference from the sites of old fallow land. All differences were best explained by the successional age of the sites. Both early stage and old fallow land showed a high proportion (>25%) of stage-specific species, but more threatened species were specific to old fallow land. We conclude that up to now the importance of old fallow land has been underestimated in conservation efforts in Central Europe. Contrary to the prevailing opinion, it is at least as important for butterflies as extensively cultivated grassland. Further conversion into forest, a common habitat in the region, should be prevented. Because old fallow land has become exceedingly rare, its inclusion in management plans is urgently needed. Otherwise, we may soon lose a valuable but often overlooked part of our biodiversity.*

Consecuencias de la Sucesión en los Pastos de Cultivo Extensivo en las Comunidades de Mariposas en Europa Central Replanteamiento de Prácticas de Conservación

Resumen: *En Europa Central, los pastos de uso no intensivo y sus etapas de sucesión han declinado drásticamente en las últimas décadas, a causa de los cambios en el uso de las tierras. De todas las etapas, el barbecho antiguo es el más afectado. Aparte del decline general, es a menudo reforestado o reconvertido como pasto de cultivo, ya que se creé que esta práctica es favorable para la conservación de la biodiversidad. Sin embargo, la importancia del barbecho no ha sido investigada suficientemente y pudiera estar subestimada. Hemos examinado las poblaciones de mariposas diurnas en 14 puntos de las montañas Jura en Suiza, para evaluar la importancia relativa de pastos de cultivo extensivo, barbecho joven y antiguo y bosque joven en este conjunto. Estas etapas son comparadas utilizando metodos univariados, multivariados y cualitativos. Demostramos que los primeros 2–3 años de sucesión tienen poca influencia en la mariposa. Por lo tanto, los*

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pastos cultivados y barbecho joven son identificados, ambos, como la " etapa joven." El barbecho viejo tiene una mayor abundancia de especies significante (+32%) y heterogéneidad (+65%), y contiene mas especies de la "Lista Roja" (+48%) que la etapa joven. El bosque joven es absolutamente escaso en especies. "Cluster Analysis" y "Correspondence Analysis" tambien demuestran un gran parecido entre los puntos de etapa joven entre sí y una clara diferencia de éstos con los de barbecho viejo. El factor determinante de estas diferencias reside en la edad de los pastos. Tanto la etapa joven como el barbecho viejo tienen una alta proporción (>25%) de especies específicas, pero más especies en peligro son específicas del barbecho viejo. Nuestra conclusión es que el barbecho viejo ha sido substimado en los esfuerzos de conservación en Europa Central. Contrariamente a la opinion que prevalece, es al menos tán importante para las mariposas como el pasto de cultivo extensivo. Su conversión en bosque, sin embargo, ha de ser prevenida. Al haberse convertido el barbecho viejo en una rareza, su inclusion en las practicas de conservación es urgente. Si no es así, tal vez perdamos pronto una valiosa pero poco reconocida parte de nuestra biodiversidad.

Introduction

As a result of land-use changes, extensively cultivated calcareous pastures and leys, which are generally considered the grassland biotope with the highest conservation value (Blab & Kudrna 1982; Bignal & McCracken 1996), are becoming increasingly rare in Central Europe (e.g., Zoller & Bischof 1980; Willems 1982; Ratcliffe 1984; World Conservation Monitoring Centre 1992; Fischer & Stöcklin 1997). Often, formerly extensively used grasslands are either converted to intensive agriculture or are abandoned and consequently convert into forests. Little is known, however, of the relative importance of the different seral stages of extensively cultivated land. There is a general belief that fallow land, at least when older, is less valuable than land still under cultivation (Walther 1995). This belief could stem from the old attitude that "wild" means "bad" by definition (Thielcke 1973) or from a strong subjective weighting of charismatic groups such as orchids or lycaenid butterflies that suffer from succession.

Well-founded studies regarding the effect of succession of extensively grazed or mown grassland on animals are scarce, and those that exist are contradictory. Thomas (1991) demonstrated a negative effect of succession on a number of lycaenid butterflies. Erhardt (1985*a*; 1985*b*) found that butterflies in the subalpine region increased in species numbers during early succession but then decreased as soon as bushes began to invade. Beinlich (1995) found a maximum of butterfly species in early to intermediate seral stages, but it is unclear what "intermediate" means in his study. On the other hand, a slight increase of species numbers throughout succession was observed in spiders (A. Hänggi, personal communication). Both Erhardt and Hänggi point out the presence of rare species only in late seral stages. Most other work in this field focuses on the succession from rather species-poor arable land or corn fields (e.g., Southwood et al. 1979) and not from highly diverse, extensively grazed pastures or extensively mown leys.

More thorough investigations of this neglected subject are desperately needed because the problem of fallow land has shifted greatly during the last two decades. Surber et al. (1973) warned about too much fallow land; now such land has decreased significantly in Central Europe and has almost disappeared from many areas, particularly in lowland regions, for two main reasons. First, intensification of cultivation or afforestation has reduced the land area that can fall fallow (Hegg et al. 1993). Second, remaining fallow land is often recultivated, because conservation practitioners focus their efforts on managing the initial stage of cultivated grassland, making fallow land even rarer. Old fallow land has now become so rare in the Jura mountains of northwestern Switzerland and adjacent France that only three suitable sites could be found for this study in an area of approximately 1000 km^2.

We are in serious danger of losing that often overlooked part of our biodiversity associated with fallow land without realizing it, and there is an urgent need for information on how important these habitats are for biodiversity. Consequently, we examined the relative importance of the different stages of succession and compared the lepidopteran faunas of 14 sites in four different stages of a sere, from extensively grazed calcareous pastures to woodland. We aimed to answer the following questions: (1) Do the stages differ in their species numbers and in diversity? (2) Do different seral stages support distinct butterfly communities? (3) Do certain species or species groups depend on specific stages for survival? From these, we can answer the larger question of how important fallow land is for butterflies.

Day-flying lepidoptera are well suited for answering these questions. They are sensitive indicators that react quickly to environmental change (Erhardt 1985*a*), and they are specious and abundant enough for meaningful analysis. Most species are rather sedentary yet are mobile enough to rapidly colonize new habitats in their close vicinity (Baker 1969), which allows meaningful samples to be obtained from relatively small areas. And, they are a charismatic group, categorized in Red Lists

(Gonseth 1994), which makes the results usable for public discussion and political action.

Methods

Study Sites

The 14 study sites were situated within 25 km of one another in the Jura Mountains to the southwest of Basel, Switzerland (Fig. 1). All sites were 1000 m² in size, faced south by southeast to south by southwest, had similar slopes, and were located at elevations between 510 and 720 m above sea level. They belonged to four consecutive seral stages of extensively grazed calcareous grassland in this region (Kienzle 1979): stage 1 (five sites investigated), extensively grazed pastures on nutrient-poor calcareous soils, phytosociologically characterized as *Mesobrometum typicum*, still cultivated; stage 2 (three sites investigated), early fallow land, no grazing for 2–3 years, grasses dominating vegetation, few woody plants present yet; stage 3 (three sites investigated), old fallow land, no grazing for approximately 10 years, loosely but evenly covered with blackthorn *Prunus spinosa* (50–60 cm in height); and stage 4 (three sites investigated), dense young forest, no grazing for approximately 20–30 years, trees replacing blackthorn, up to 4 m in height.

The results of surveys in stage 4 sites were not directly comparable to those from other stages because the dense nature of these sites required a different censusing method. Stage 4 therefore was included only for crude comparison in parts of the analysis where explicitly mentioned, to assess the effect of continuing late succession (Table 1). The sites of stage 3 included in this investigation represent all south-facing sites of the desired minimal size that could be found in the region within an area of approximately 1000 km². North-facing sites are even rarer because they have been converted to agricultural land due to their richer soils.

Surveys

From 6 June to 11 September 1997, numbers of diurnal macrolepidoptera (Rhopalocera, Zygaenidae, and Geometridae) were surveyed on all sites once a week. This is the optimal period for butterflies in the investigated region. During a 2-week period (23 June–6 July) no sites were surveyed due to bad weather conditions. Thus, 13 weeks were included in the analysis. For the statistical analysis the weekly counts per species and site were added up as a measure of presence of a species at each site during the sampling season. Due to bad weather, some individual surveys were lacking; we estimated their values by interpolation by the method of Hall (1981).

We conducted area transect surveys (i.e., sites patrolled in a serpentine pattern, corridors 5 m wide) so that each part of the survey area was covered by the butterfly net once. We chose this method because all stage 3 sites were too small (each about 1000 m²) for conducting linear transects. Larger stage 3 areas no longer exist in the region. All butterflies within reach of the net were identified. Multiple counting of individuals of active species could not be avoided but was not problematic because sites rather than species (which have differential catchability) were compared to each other and the error was the same in all sites. An adequate plot size was shown to be 1000 m² (Balmer 1999). Due to the density of the stands in stage 4 sites, linear transect surveys were conducted and the data were extrapolated to the same total area as in the first three stages. Transects were made only in good weather
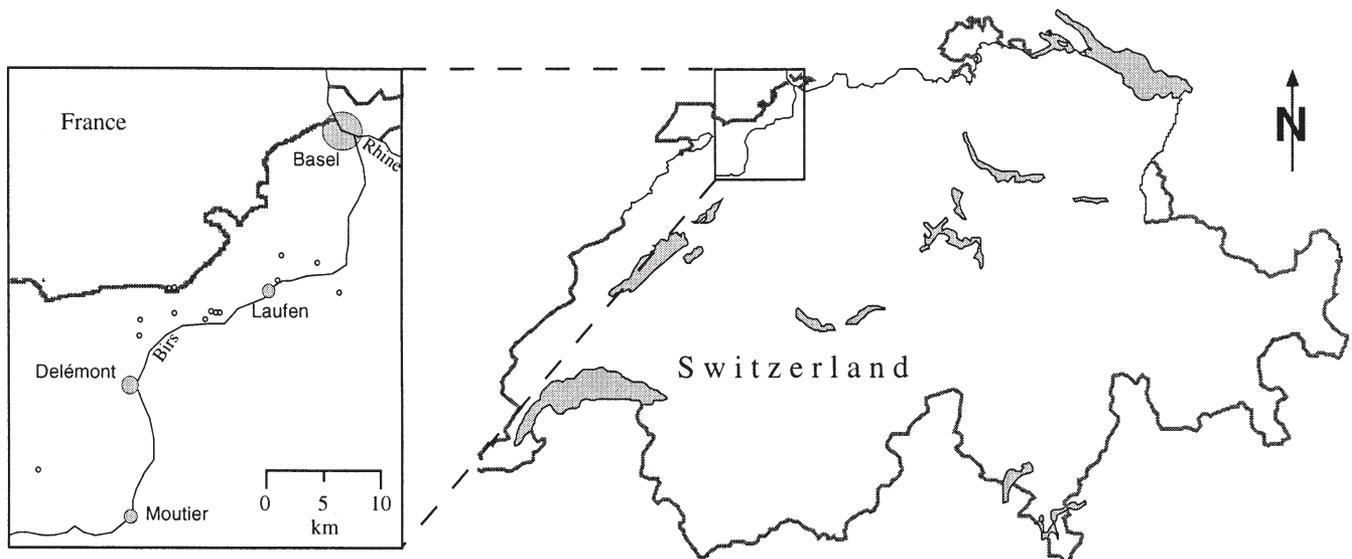

Figure 1. Location of the 14 study sites in the Jura Mountains (small dots).

Table 1. Characterization and codes of the 14 study sites in the Jura Mountains.

Seral stage	Habitat	Location	Code	Age[a]	Elevation (m)
1	extensively grazed pasture dominated by herbs	Blauenweide	1B	0	630
		Kiffis (France)	1K	0	640
		Liesberg	1L	0	510
		Nenzlingen	1N	0	520
		Réselle de Soyhières	1R	0	550
2	early fallow land dominated by grass	Himmelried	2H	2	570
		Liesberg	2L	3	570
		Vorbourg	2V	2	540
3	old fallow land dominated by blackthorn	Kiffis (France)	3K	10[b]	610
		Liesberg	3L	10[b]	580
		Soulce	3S	10[b]	720
4	young forest dominated by young trees	Combe de Movelier	4C	20[b]	590
		Dittingen	4D	20[b]	400
		Liesberg	4L	20[b]	590

[a] *Years without grazing.*
[b] *Approximation.*

between 1000 and 1700 hours. The sequence of surveys was alternated to avoid systematic effects of time of day.

Diversity Measures

The three seral stages (or four, where mentioned) were compared. To examine whether the seral stages differed in their diversity, we calculated species richness (S) and the abundance of individuals (N) for every site. To exclude bias of species richness imposed by differential sample sizes (Peet 1974), we also calculated rarefied species richness (Sanders 1968, as corrected by Simberloff 1971), which is a measure estimating how many species would have been found with a lesser and standardized number of individuals. Heterogeneity (often called "diversity") was calculated as Fisher's α (Fisher et al. 1943), which is the parameter of the logarithmic distribution. To check whether abundances of the species present followed a logarithmic distribution as needed for Fisher's α to be meaningful, we drew Whittaker plots (Krebs 1989) for visual inspection. Evenness was calculated as modified Hill's ratio $F_{2,1}$ (Alatalo 1981; Appendix 1), a measure that gives little weight to the rare species and that avoids underestimation of species richness (Peet 1974) because it uses no estimate of species richness (Alatalo 1981). Evenness measures how evenly the individuals of a sample are distributed over the species present in the sample.

These measures were compared between the seral stages by means of one-way analysis of variance. Posthoc comparisons between pairs of stages were performed with a Scheffé test on a significance level of $p < 0.05$. Pairwise comparisons between stages 1 and 2 combined (hereafter stage 1+2) and stage 3 were performed with an unpaired t test (Zar 1984). All calculations were performed with the program StatView, Version 4.51 (Abacus Concepts 1995).

Community Resemblance

To investigate differences in species composition between stages, we further analyzed data by classification and ordination methods. Both classes of methods group the sites according to the resemblance they have to one another. Matrices of pairwise similarities between sites were constructed with Morisita's index (Morisita 1959, Appendix), and a cluster analysis was performed on these with the average linkage algorithm unweighted pair-group method using arithmetic averages (UPGMA) as described in Krebs (1989). Morisita's index is probably the best similarity measure for ecological use because it is nearly independent of sample size and diversity (Wolda 1981).

To confirm and refine the results obtained by cluster analysis, we performed a correspondence analysis on the untransformed data set using the program JMP, Version 3.2.2 (SAS Institute 1997). The consecutive axes produced by this method (ordination axes) explain a decreasing proportion of the observed variance in the data, with the first axis explaining the greatest proportion, the second explaining the greatest proportion of the remaining variance, and so forth.

Species Reactions

In a last step, we compared the lists of species abundances qualitatively to investigate the effects of succession on a single species or group of species. For each species, we calculated the average abundance and the relative frequency (in percent) per seral stage. Using chi-square statistics, we then determined whether the average abundances deviated from an expected uniform distribution. Where they did, we assigned the species to the seral stage(s) of most frequent occurrence and defined it as "specific to this/these stage(s)." Otherwise the species was considered not stage-specific.

Where the numbers of individuals were too small to perform meaningful chi-square statistics, species were assigned to the stages, or not assigned at all, in accordance with the following criteria. Species with more than 30 individuals and relative frequencies between 40% and 60% in both stage 1+2 and stage 3 were considered specific to both stages. To be assigned to one of the stages, a species needed to meet three conditions: its relative frequency in the stage had to be above 75%, its mean abundance in the stage had to be >1, and, to avoid assignment of a species to a specific stage that was actually specific to a location, it could not be confined to a single location. The classification made was based solely on the data, because the classifications in the literature address different habitat types from the ones we investigated.

Results

Diversity Measures

A total of 6358 butterflies belonging to 82 species was recorded during the study period (Table 2), the fourth seral stage not included. The three successional stages differed significantly in their Fisher's α and rarefied species richness, whereas species richness, modified Hill's ratio $F_{2,1}$, and abundance were not significantly different. Post-hoc comparisons between the stages revealed that stage 1 and stage 2 were not different from each other in any of the investigated measures. The overall significances were always due to a significant difference of stage 3 (Table 3). The same was true for the trends in species richness and the number of Red List species.

Stages 1 and 2 were thus grouped into one single stage (see discussion), and the two resulting stages (stage 1+2 and stage 3) differed significantly in their species richness and in their number of Red List species (Fig. 2).

Whittaker plots confirmed that the species abundances followed a logarithmic distribution in all sites (data not shown). Fisher's α was therefore an appropriate measure of heterogeneity.

Although stage 4 was not directly comparable to the other stages, it was different from other stages because it had dramatically lower numbers of species and individuals (Table 2). Except for two species (*Boarmia ribeata*, Geometridae, and *Philereme transversata*, Geometridae, each found once), all species found in stage 4 were also found in other stages. Stage 4 was not included in any further analyses.

Community Resemblance

The dendrogram produced by the cluster analysis grouped into one cluster all sites of stages 1 and 2 except site 1N. The sites of stage 3 and site 1N did not all cluster together but were clearly separated from the "stage 1 and 2 cluster" (Fig. 3). Of the four sites outside the stage 1 and 2 cluster, sites 3K and 3L built a second cluster. As in the univariate analysis, stages 1 and 2 were not distinguishable, whereas stage 3 was clearly different.

The ordination (correspondence analysis) produced similar results. A biplot of ordination axes 1 and 2 again showed a grouping of the sites of stages 1 and 2, with site 1N being slightly more distant. The sites of stage 3 were clearly separated from these (Fig. 4). Sixty-two percent of the observed variance was explained by the first three ordination axes.

Ordination axis 1 separated a homogenous first group of all sites of stages 1 and 2 from the three sites of stage 3. Site 3S was furthest away from the first group. The scores of stage 3 were significantly different from those of stage 1+2. Ordination axis 2 separated sites 3S and 1N from a group with all other sites. Sites 3K and 3L lay at the edge of this group in the opposite direction from site 3S. Ordination axis 3 showed the same groups as axis 2, with only a change in position of site 1N relative to the remaining sites.

Species Reactions

The preceding steps of analysis have shown that successional stages 1 and 2 could not be distinguished by quan-

Table 2.   Summary of diversity measures of the investigated butterfly communities in the Jura Mountains for each study site.

	Study site[a]													
	1B	1K	1L	1N	1R	2H	2L	2V	3K	3L	3S	4C	4D	4L
Species richness	27	28	44	31	37	27	30	38	43	50	37	2	4	5
Abundance[b]	387	593	674	655	823	438	420	1103	423	560	282	3	7	13
Fisher's α	6.61	6.11	10.54	6.76	7.96	6.36	7.39	7.63	11.97	13.28	11.39	—	—	—
Rarefied species richness[c]	23.6	23.5	33.3	24.9	27	22.8	25.4	28.1	37.5	36.5	36.1	—	—	—
Modified Hill's ratio $F_{2,1}$	0.67	0.41	0.51	0.53	0.54	0.53	0.54	0.43	0.52	0.45	0.71	—	—	—
Number of Red List species[d]	6	4	7	6	9	4	7	6	9	9	9	0	1	0

[a] *Sites of stage 4 are included for comparison but are not strictly comparable (see text). See Table 1 for site codes.*
[b] *Number of butterflies recorded in 13 transects.*
[c] *Rarefied to N = 253.*
[d] *Categories 1–4 in the Red Data Book of threatened butterflies of Switzerland (Gonseth 1994).*

Table 3.   Probability values of analysis of variance (ANOVA) and post-hoc comparisons[a] of the diversity measures of the butterfly communities in seral stages 1–3 in the Jura Mountains.

		Post-hoc comparison between pairs of seral stages		
	Overall ANOVA	1, 2	1, 3	2, 3
Species richness	0.116	0.938	0.184[b]	0.160[b]
Abundance[c]	0.435	0.988	0.520	0.511
Fisher's α	0.003	0.901	0.006[b]	0.007[b]
Rarefied species richness[d]	0.004	0.908	0.007[b]	0.008[b]
Modified Hill's ratio $F_{2,1}$	0.775	0.905	0.938	0.776
Number of Red List species[e]	0.055	0.803	0.117[b]	0.072[b]

[a] Scheffé's F test, p < 0.05.
[b] Interstage differences responsible for the significance or trend in the overall ANOVA of an index.
[c] Number of butterflies recorded in 13 transects.
[d] Rarefield to N = 253.
[e] Categories 1–4 in the Red Data Book of threatened butterflies of Switzerland (Gonseth 1994).

titative measures. Comparison of the specificity of the recorded species to the investigated stages yielded similar results. Few species were specific to either stage 1 (5 species) or stage 2 (2 spp.), whereas many were specific to both stage 1 and 2 (14 spp.) or to stage 3 (19 spp.). Hence the separation of stage 1 and stage 2 is not justified in the context of this study, and their combination to a single group called stage 1+2 is appropriate. Of the 82 recorded species, 21 (25.6%) each were specific to stage 1+2 and to stage 3 (Table 4). The remaining species either were equally distributed over the stages (7 species, 8.5%) or could not be assigned to a stage due to low abundance or ambiguous distribution (33 spp., 40.2%). Some species assigned to stage 1+2 showed a clear preference for either stage 1 or stage 2 (Table 4).

One family (Lycaenidae) showed a strong affinity to stage 1+2; six species were specific to this stage and none were specific to stage 3. Of the species specific to one stage, five that were in stage 1+2 are on the Red List of threatened butterflies of Switzerland (Gonseth 1994), which is 38.5% of the stage-specific species from families for which Red Lists exist. There are no Red Lists for the Geometridae and Zygaenidae in Switzerland. In stage 3, eight specific species, or 57.1% of all possible stage-specific species, are on the Red List. *Pyronia tithonus, Gonepteryx rhamni, Issoria lathonia, Coenonympha glycerion*, and *Pseudoterpna pruinata* exhibited a strong local (as opposed to stage) specificity, occurring in all stages but only on sites in Kiffis and Liesberg.
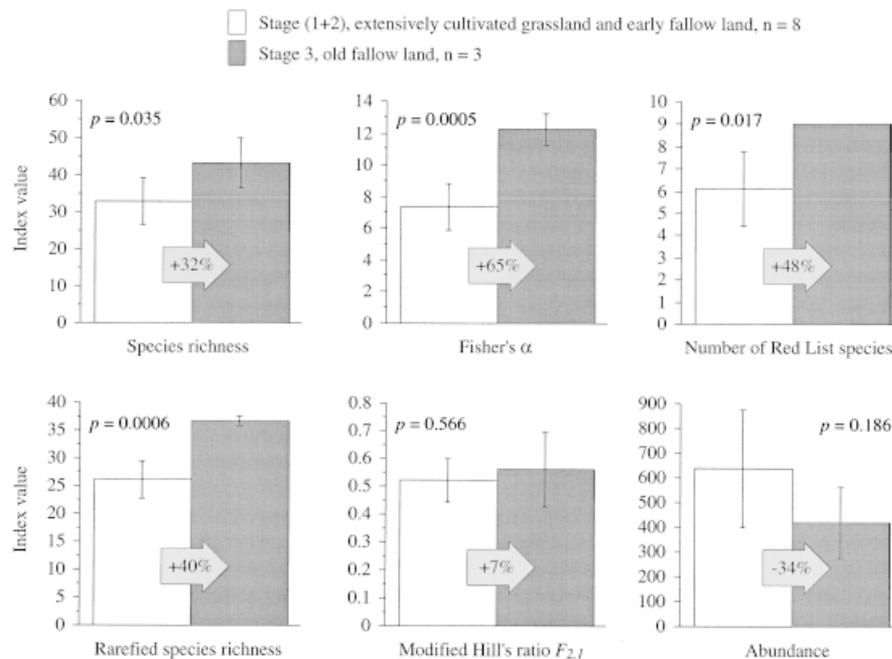

Figure 2. Changes in diversity measures of butterfly populations, with seral stage in the two stages found to be relevant (error bars indicate SD).
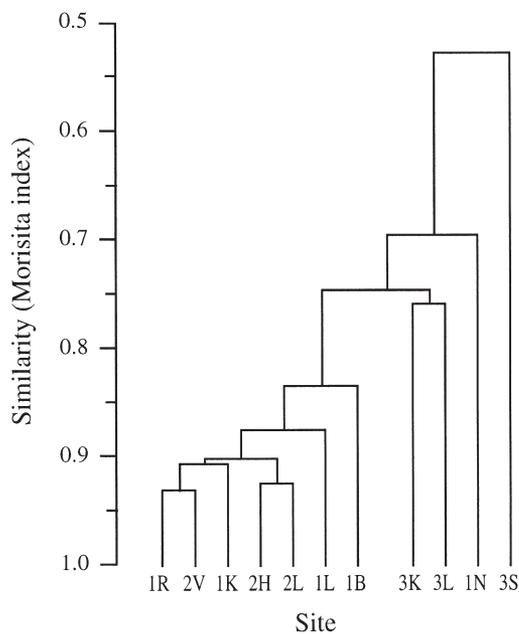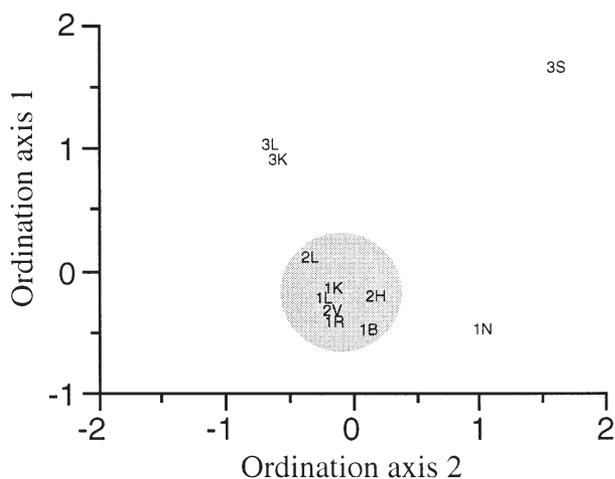
Figure 3. Dendrogram of cluster analysis (UPGMA) using Morisita similarity index for the butterfly communities of the investigated sites in the Jura Mountains. The shorter the connection between two sites in the diagram, the more similar the sites are. Sites are divided into two groups to highlight the separation of the stage 3 sites. Site codes defined in Table 1.

Discussion

Similarity of Early Seral Stages

Seral stages 1 and 2 did not differ in diversity or in species composition as measured by both cluster analysis and or-

dination. The only difference we found concerned a few species that showed a specificity to one of the stages. This difference between the two stages is minor, however, compared to their difference from stage 3 and could be explained in part by chance or local effects. For butterflies, stage 1 and stage 2 are practically the same, most likely because during the initial phase of succession plant species composition changes little. There is only a change in dominance; grasses increase and herbs decrease in density. There is also a change in structure as the sward gets matted (Kienzle 1979). In the investigated area this structural change seems less important for butterflies than the presence of their larval food plants. Hence the distinction between the two initial successional stages is not biologically justifiable in the investigated area with respect to butterflies. The proper stages for comparison are stage 1+2, stage 3, and stage 4.

These findings seem to contradict those of Thomas (1991) who found dramatic effects on certain butterfly species at the beginning of succession. But as Thomas (1998) points out in the case of *Maculinea arion*, niches occupied change with both latitude and elevation. Notably, our data suggest that *M. arion* is specific to early fallow land in the investigated area, not to cultivated grassland as in southern England. It seems that in the warmer, south-facing slopes of the Jura Mountains, the decline in above-ground temperature due to the growth of higher swards has much weaker effects on butterflies than it does in cooler regions. Temperature does not seem to be a limiting factor.

Diversity

A comparison of the stages reveals that both species richness and heterogeneity increase significantly from
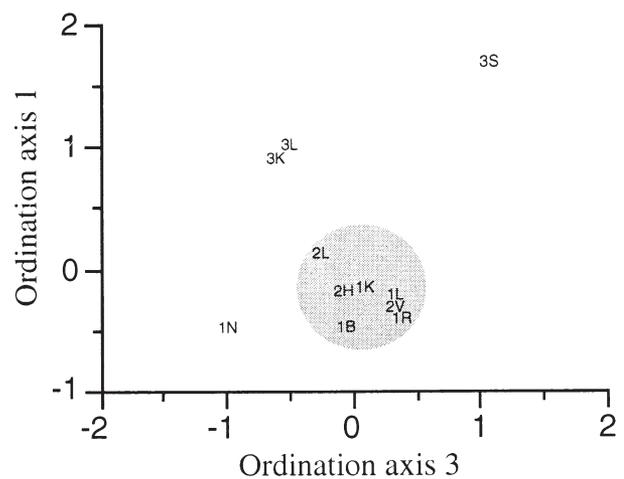

Figure 4. Ordination (correspondence analysis) diagram of the butterfly communities of the investigated sites in the Jura Mountains. Axes are site scores of the first three ordination axes. The closer two sites are to each other in the diagram, the more similar they are in their species composition. Circles are drawn arbitrarily to highlight the grouping of the sites. Site codes are defined in Table 1.

Table 4. List of all diurnal butterfly species recorded during the study period arranged by the seral stage they were found to be specific to in the Jura Mountains.

Specificity	Species[a]	N	Stage 1 + 2[b] (n = 8)	Stage 3[b] (n = 3)	χ^{2c}	Status[d]
Stage 1 + 2	*Maniola jurtina*	1928	205.3 (68.3)	95.3 (31.7)	40.2***	
	Melanargia galathea	621	72.1 (83.1)	14.7 (16.9)	38.0***	
	Clossiana dia	276	34.1 (97.1)	1.0 (2.8)	31.2***	2
	Zygaena filipendulae	291	34.9 (89.7)	4.0 (10.3)	24.5***	
	Lysandra bellargus	309	36.6 (87.3)	5.3 (12.7)	23.3***	
	Polyommatus icarus	164	20.3 (96.8)	0.7 (3.2)	18.3***	
	Ortholitha bipunctaria	169	20.8 (95.4)	1.0 (4.6)	17.9***	
	Idaea serpentata	199	22.9 (81.1)	5.3 (18.9)	10.9***	
	Colias alfacariensis	101	12.4 (94.9)	0.7 (5.1)	10.5**	
	Aspilates gilvaria	97	11.9 (94.7)	0.7 (5.3)	10.0**	
	Idaea macilentaria[e]	82	10.1 (96.8)	0.3 (3.2)	9.2**	
	Idaea rufaria[e]	43	5.4 (100)	—	—	
	Spialia sertorius	42	5.3 (100)	—	—	
	Aricia agestis	38	4.8 (100)	—	—	3
	Plebicula dorylas[e]	39	4.8 (93.4)	0.3 (6.6)	—	3
	Pyrgus armoricanus[e]	26	3.3 (100)	—	—	2
	Jordanita globulariae[e]	40	4.6 (82.2)	1.0 (17.8)	—	
	Cyaniris semiargus	17	2.0 (85.7)	0.3 (14.3)	—	
	Scopula immorata	41	4.6 (77.6)	1.3 (22.4)	—	
	Maculinea arion[f]	9	1.1 (100)	—	—	3
	Thanaos tages[f]	9	1.1 (100)	—	—	
Stage 3	*Aphantopus hyperantus*	249	8.6 (12.6)	60.0 (87.4)	38.5***	
	Pyronia tithonus	139	4.1 (10.5)	35.3 (89.5)	24.7***	2
	Pieris napi	43	1.4 (11.4)	10.7 (88.6)	7.2**	
	Coenonympha glycerion	61	2.9 (18.5)	12.7 (81.5)	6.2*	2
	Ortholitha chenopodiata	93	5.4 (24.4)	16.7 (75.6)	5.8*	
	Coenonympha arcania	28	—	9.3 (100)	—	4b
	Cidaria tristata	31	0.3 (2.5)	9.7 (97.5)	—	
	Erebia aethiops	24	0.3 (3.3)	7.3 (96.7)	—	3
	Callophrys rubi	15	0.1 (2.6)	4.7 (97.4)	—	2
	Cidaria bilineata	21	0.8 (13.0)	5.0 (87.0)	—	
	Mellicta parthenoides	25	1.1 (17.4)	5.3 (82.6)	—	3
	Ortholitha plumbaria	16	0.5 (11.1)	4.0 (88.9)	—	
	Pseudopanthera macularia	7	—	2.3 (100)	—	
	Argynnis paphia	9	0.1 (4.5)	2.7 (95.5)	—	
	Ochlodes venatus	14	0.5 (13.0)	3.3 (87.0)	—	
	Araschnia levana	7	0.1 (5.9)	2.0 (94.1)	—	
	Cidaria alternata	7	0.1 (5.9)	2.0 (94.1)	—	
	Carterocephalus palaemon	4	—	1.3 (100)	—	
	Nemeobius lucina	4	—	1.3 (100)	—	3
	Scopula nigropunctata	4	—	1.3 (100)	—	
	Brenthis daphne	13	0.6 (19.0)	2.7 (81.0)	—	2
Both stages	*Thymelicus sylvestris*	103	9.5 (51.4)	9.0 (48.6)	0.0	
	Coenonympha pamphilus	223	20.6 (51.6)	19.3 (48.4)	0.0	
	Ematurga atomaria	104	8.9 (44.7)	11.0 (55.3)	0.2	
	Idaea humilata	248	24.4 (58.0)	17.7 (42.0)	1.1	
	Pieris rapae	40	3.6 (49.7)	3.7 (50.3)	—	
	Lysandra coridon	32	2.9 (48.9)	3.0 (51.1)	—	3
	Brintesia circe	35	2.9 (41.8)	4.0 (58.2)	—	2

continued

stage 1+2 to stage 3 and then decrease dramatically to stage 4. Thus from a butterfly conservationist's point of view, stage 3 is most valuable, and continued succession to forest should be prevented. This point is strengthened by the fact that stage 3 is much rarer than stage 4 in the investigated region.

Because heterogeneity combines two concepts—species richness and evenness (Krebs 1989)—it can be determined which of these is responsible for the detected change in heterogeneity. Evenness was the same in all stages, whereas species richness changed. Thus the increased heterogeneity in stage 3 was due to increased richness and was not a consequence of a change in the dominance distribution of the species assemblages.

Greater species richness in stage 3 was remarkable for

Table 4.   (continued)

Specificity	Species[a]	N	Stage 1 + 2[b] (n = 8)	Stage 3[b] (n = 3)	χ^{2c}	Status[d]
Not assigned	*Lasiommata megera*	29	3.0 (64.3)	1.7 (35.7)	—	
	Scopula ornata	32	2.0 (27.3)	5.3 (72.7)	—	
	Issoria lathonia	4	0.4 (52.9)	0.3 (47.1)	—	
	Leptidea sinapis	16	1.5 (52.9)	1.3 (47.1)	—	
	Pseudoterpna pruinata	11	1.0 (50.0)	1.0 (50.0)	—	
	Cidaria spadicearia	3	0.3 (42.9)	0.3 (57.1)	—	
	Gonepteryx rhamni	2	0.1 (27.3)	0.3 (72.7)	—	
	Aglais urticae	2	0.1 (27.3)	0.3 (72.7)	—	
	Minoa murinata	10	0.8 (36.0)	1.3 (64.0)	—	
	Thalera fimbrialis	6	0.6 (65.2)	0.3 (34.8)	—	
	Scopula subpunctaria	7	0.8 (69.2)	0.3 (30.8)	—	
	Hesperia comma	17	1.8 (63.6)	1.0 (36.4)	—	
	Lycaena tityrus	14	1.5 (69.2)	0.7 (30.8)	—	
	Jordanita notata	1	0.1 (100)	—	—	
	Mellicta athalia	1	0.1 (100)	—	—	2
	Pyrgus malvae	1	0.1 (100)	—	—	3
	Scopula immutata	2	0.3 (100)	—	—	
	Perizoma albulata	3	0.4 (100)	—	—	
	Idaea ochrata	4	0.5 (100)	—	—	
	Zygaena achilleae	7	0.9 (100)	—	—	
	Hipparchia semele	11	1.3 (78.9)	0.3 (21.1)	—	2
	Semiothusa clathrata	7	0.5 (33.3)	1.0 (66.7)	—	
	Vanessa io	13	1.0 (37.5)	1.7 (62.5)	—	
	Papilio machaon	1	—	0.3 (100)	—	
	Plebicula thersites	1	—	0.3 (100)	—	3
	Thecla betulae	1	—	0.3 (100)	—	
	Vanessa atalanta	1	—	0.3 (100)	—	
	Opisthograptis luteolata	1	—	0.3 (100)	—	
	Philereme vetulata	1	—	0.3 (100)	—	
	Sterrha muricata	1	—	0.3 (100)	—	
	Ortholitha moeniata	2	—	0.7 (100)	—	
	Fixsenia pruni	3	—	1.0 (100)	—	1
	Satyrium acaciae	3	—	1.0 (100)	—	2

[a] *Sorted by strength of specificity where possible. See Methods section for criteria of assignment to the stages.*
[b] *Mean abundance per stage. Weighted proportions of the total abundance (percentage) in parentheses.*
[c] *Chi-square value of interstage difference of mean abundance, where calculable. Significance levels: *p < 0.05; **p < 0.01; ***p < 0.001; no asterisk, p > 0.05; —, abundance too low for χ^2 calculation.*
[d] *Categories in the Red Data Book of threatened butterflies of Switzerland (Gonseth 1994).*
[e] *Specific to stage 1.*
[f] *Specific to stage 2.*

two reasons. First, the sites of stage 3 had smaller total areas (transect area plus the area of immediately adjacent land of identical type). Second, the abundances of butterflies in stage 3 sites were smaller on average than in stage 1+2. It would therefore be predicted by island biogeography theory (MacArthur & Wilson 1967) that stage 3 should have a lower species richness than the "bigger" sites of stage 1+2. The richness of stage 3 can thus be expected to be even a bit underestimated relative to that of stage 1+2.

The results are even clearer when one looks at rarefied species richness. The difference in species richness between stage 1+2 and stage 3 becomes even more pronounced if the different abundances are taken into account. Even though the different abundances are themselves indisputably a characteristic of the communities, this strengthens the point made above that the

real richness of stage 3 (estimated from fewer individuals on average) is underestimated relative to that of stage 1+2.

To preclude the possibility that the observed differences of diversity are the consequence of some other confounding factor and not of successional age, we offer the following considerations: (1) A stepwise regression showed that all measured changes were best explained by seral stage and were not or were much less correlated to the other recorded factors of total area, distance to forest, elevation, latitude, or longitude (Table 5). (2) The dramatic decrease of species richness from stage 3 to stage 4 demonstrated that the habitat quality of stage 3 must in itself be the reason for its increased richness, not any underlying factor also present in later seral stages. (3) Also, the findings cannot be attributed to the inclusion of the Geometridae, whose larvae feed on woods, because their omission did not alter these findings (data not shown).

Table 5.   Results of stepwise regressions[a] with species richness, Fisher's α, and the first three ordination axes as dependent variables showing which environmental factors determine the diversity and species composition of the investigated butterfly communities in the Jura Mountains.

			Model		
Dependent variable	*Explanatory variable[b]*	F	*variable(s) included*	r^2	p
Species richness	successional age (SA)	14.07	SA	0.351	0.055
	elevation (EL)	13.40	SA + EL	0.644	0.016
	longitude (LO)	4.93	SA + EL + LO	0.791	0.009
Fisher's α	successional age (SA)	51.82	SA	0.689	0.002
	distance to forest (DF)	16.57	SA + DF	0.827	0.0009
	total area (TA)	6.17	SA + DF+ TA	0.908	0.0005
Ordination axis 1	successional age (SA)	80.12	SA	0.909	<0.0001
	latitude (LA)	5.08	SA + LA	0.944	<0.0001
Ordination axis 2	no variable with significant effect				
Ordination axis 3	latitude (LA)	25.64	LA	0.597	0.005
	successional age (SA)	9.81	LA + SA	0.747	0.004
	elevation (EL)	4.03	LA + SA + EL	0.839	0.004

[a] *Foreward procedure, F-to-enter = 4, F-to-remove = 3.996, see methods section for variables tested.*
[b] *Only explanatory (i.e., independent) variables with significant effect on the dependent variable (F ≥ 4) are listed in order of decreasing influence on the dependent variable. "Seral stage" is changed to "successional age" because a continuous variable is needed for stepwise regression.*

Communities

Both classification and ordination showed that all stage 1+2 sites were similar to one another in species composition and that stage 3 sites were clearly distinct from these but not quite as similar to each other. A comparison of the correspondence analysis site scores to successional age and other possible explanatory factors by stepwise regression showed that successional age was the factor determining the position of the sites on the first ordination axis, which explains the greatest part of the observed variation in the data. Ordination axis 2 cannot be explained by the environmental factors measured and seems primarily to reflect the presence of special dominant species in sites 1N and 3S. Ordination axis 3 might represent a geographical component because the scores correlated best with latitude. But this correlation is probably due mainly to the high leverage of site 3S and has to be treated with caution (Table 5).

Site 1N appeared to differ from the other stage 1+2 sites. Although on the first (and most important) ordination axis it was perfectly grouped with all other sites, showing that it is in essence of the same type, the other ordination axes and the cluster analysis clearly separated it. The separation on ordination axis 2 is mainly an effect of a single geometrid species, *Idaea macilentaria*, which is abundant in Nenzlingen but was seen elsewhere on only one occasion. If this species is omitted from the analysis, site 1N is much closer to the other sites of stage 1+2 on the second ordination axis. It does not change the result of the cluster analysis, however, which is robust against influences of single species. The difference in 1N may also be due to its somewhat richer soil and the resulting higher and denser sward compared to other sites of stage 1+2. Aside from the abundant species that dominated most sites (i.e., *Maniola jurtina*,

Melanargia galathea), no other single species exerted a substantial effect on the outcome of the correspondence and cluster analyses. This shows that the results are based on real and strong patterns and not on random effects.

Species Level

The butterfly groups included in this study had a high level (>50%) of specificity to seral stages. More than 25% of the species each were specific to either stage 1+2 or stage 3. This shows the specific habitat requirements of many species. They require a certain seral stage for survival and cannot simply switch to another stage. Because we were cautious and did not assign many species to a seral stage, the real number of stage-specific species may be higher. There were relatively few generalists, which implies that butterflies react strongly to environmental change and hence are good indicators of habitat change (Erhardt 1985*a*).

A high proportion of the specific species in both stages is included in the Red List of threatened butterflies of Switzerland. Because Red Data Books of Central Europe mainly contain specialist species whose habitats are or have become rare, the proportion of Red List species is a good indicator of the status of the respective habitat. The successional stages included in this study seem to be highly endangered.

Stage 1+2 is essential for lycaenids. This confirms the results of many other studies showing that lycaenids are in general thermophilous and bound to sunny habitats where their larval food plants occur (Lepidopterologen-Arbeitsgruppe 1987; Thomas 1991).

The large number of Red List species in both stage 1+2 and stage 3 provides an impetus for effective protection of these habitats, especially in countries such as

Switzerland, where Red Lists are by law a binding means for nature conservation. The fact that stage 3 hosts significantly more Red List species than early seral stages of course does not lead to the conclusion that all extensively cultivated grassland should be abandoned. Rather, it emphasizes that later seral stages deserve and require equal protection at minimum. With respect to butterflies, removal and recultivation of old fallow land is the wrong conservation strategy if it is not combined with other measures to achieve a good mixture of various seral stages. The observation that some species show a specificity to certain locations rather than seral stages is a reminder that, besides the habitat effect with which this paper is mainly concerned, there are also other geographical and historical influences on present day species communities. Local processes acting at the habitat level may be overridden by regional processes acting on larger spatial or temporal scales, for instance processes mediated through dispersal ability or natural barriers (Ricklefs 1987).

Conservation Implications

Extensively cultivated pastures and leys have long been recognized as important habitats that need protection. Our study shows once more that they are host to many specific and Red List butterfly species. Different from these habitats, old fallow land (stage 3 in this study) has so far attracted little attention for nature conservation. We have shown, however, that it has a distinct butterfly fauna, is even richer in species, is more diverse, and comprises more threatened butterfly species than calcareous pastures (stage 1) and early fallow land (stage 2). Moreover, old fallow has become rare in Central Europe, emphasized by the fact that, within an area of approximately 1000 km^2, the three sites included in this study are the only ones left of this vegetation type worth mentioning. When old fallow land becomes forest, virtually all butterfly diversity is lost. Even though forests have high conservation value for other groups, this conversion should be prevented because forests, unlike the other stages we investigated, are by no means rare in the region.

There is an urgent need to rethink conservation priorities. Later successional stages must be included in any management plan for conservation areas. A management approach that includes all nonforest seral stages at the same time is crucial. We recommend a rotation management (Duffey et al. 1974) that includes both extensively cultivated and old fallow land (10 years of age) but that prevents succession of land to forest. This management scheme is problematic because it requires relatively large areas. But it has the great advantage of reducing management effort because the single compartments of a conservation area can be left alone for longer periods of time.

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Appendix

Formulae used in analysis of butterflies in the jura mountains.

Rarefied species richness (Sanders 1968, as corrected by Simberloff 1971):

$$S_{\mathrm{rar}} = \sum_{i=1}^{S} \left[1 - \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right],$$

where S is the total number of species in the entire collection, N is the total number of individuals in the entire collection, N_i is number of individuals in species i, and n is value of sample size chosen for standardization ($n \leq \mathrm{minimum}(N_i)$).

Fisher's α (Fisher et al. 1943):

$$\alpha = \frac{N(1 - x)}{x},$$

where x is approximated iteratively by solving

$$\frac{S}{N} = \frac{1 - x}{x} [-\log_e (1 - x)],$$

(N, S as in rarefied species richness calculation).

Modified Hill's ratio (Alatalo 1981):

$$F_{2,1} = \frac{(N_2 - 1)}{(N_1 - 1)},$$

where $N_1 = \exp H'$ and $H' = -\Sigma(p_i \log_e p_i)$ (Shannon-Wiener index); $N_2 = 1/\Sigma p_i^2$; and p_i is the frequency of species i.

Morisita's similarity index (Morisita 1959):

$$C_\lambda = \frac{2\Sigma(X_{ij}X_{ik})}{N_j N_k \left[\dfrac{\Sigma(X_{ij}(X_{ij} - 1))}{N_j(N_j - 1)} + \dfrac{\Sigma(X_{ik}(X_{ik} - 1))}{N_k(N_k - 1)} \right]},$$

where X_{ij} and X_{ik} are the number of individuals of species i in sample j and sample k, respectively; $N_j = \Sigma X_{ij}$ (total number of individuals in sample j); and $N_k = \Sigma X_{ik}$ (total number of individuals in sample k).