Influence of forest and grassland management on the diversity and conservation of butterflies and burnet moths (Lepidoptera, Papilionoidea, Hesperiidae, Zygaenidae)

T. Schmitt

Schmitt, T., 2003. Influence of forest and grassland management on the diversity and conservation of butterflies and burnet moths (Lepidoptera, Papilionoidea, Hesperiidae, Zygaenidae). *Animal Biodiversity and Conservation*, 26.2: 51–67.

Abstract

Influence of forest and grassland management on the diversity and conservation of butterflies and burnet moths (Lepidoptera, Papilionoidea, Hesperiidae, Zygaenidae).— The distribution of butterflies and burnet moths was investigated at 38 patches in the Oettinger Forst (Bavaria, Germany) in 2001. Forty–two butterfly and four burnet moth species were recorded. They were unequally distributed over the study area. The diversity was significantly lower in the forests than in the non–forest patches. Windblows and meadows showed largely similar results but clearings had higher Shannon indices and Eveness and presented a trend to higher species numbers. The hay meadows had higher mean incidences of the 25 common species and exhibited a trend to higher numbers of individuals and species as well as higher mean Shannon indices than in the mulched meadows. The old quarries and sandpits harboured remarkable species, some of these occurring in high densities, thus underlining the conservation value of such structures in a non–target area for nature–conservation measurements.

Key words: Butterfly conservation, Meadows, Windblows, Clearings, Quarries, Sandpits.

Resumen

Influencia de la gestión de los bosques y las zonas de pastos en la diversidad y conservación de las mariposas diurnas y zygenas (Lepidoptera, Papilionoidea, Hesperiidae, Zygaenidae).— Se ha estudiado la distribución de las mariposas diurnas y zygenas en 38 parcelas de Oettinger Forst (Baviera, Alemania) en el año 2001. En total, se contabilizaron 42 especies de mariposas diurnas y cuatro de mariposas zygenas, cuya distribución en la zona de estudio resultó bastante irregular. La diversidad fue considerablemente inferior en las zonas boscosas en comparación con las zonas de pastos. En general, no parece que los *windblows* (áreas de un bosque donde los árboles han sido abatidos por el viento) y los prados ejerzan influencia alguna sobre las concentraciones de especies, si bien los claros presentan unos índices de Shannon y Eveness más altos y una tendencia a contar con un mayor número de especies. Los campos de heno presentan la incidencia media más alta de las 25 especies comunes y muestran una tendencia general a contar con un número superior de especies y ejemplares, así como unos índices de Shannon más elevados que los prados cubiertos de mantillo. Las antiguas canteras y arenales albergan varias especies notables, algunas de ellas en grandes densidades, lo que pone de relieve el gran valor que este tipo de estructuras desempeñan en la conservación, pese a ser zonas que no suelen tenerse en cuenta al efectuarse mediciones sobre el estado de conservación de la naturaleza.

Palabras clave: Conservación de mariposas, Prados, Windblows, Claros, Canteras, Arenales.

(Received: 19 XII 02; Conditional acceptance: 27 III 03; Final acceptance: 16 V 03)

Thomas Schmitt, Inst. für Biogeographie, Fachbereich VI, Wissenschaftspark Trier–Petrisberg, D–54286 Trier, Germany. E–mail: <u>thsh@uni-trier.de</u>

Introduction

Different habitats offer a wide variety of diverse ecological niches. While many animal and plant species have rather limited ecological capacities, many species are restricted to one or a small set of habitats (WEIDEMANN, 1986; EBERT & RENNWALD, 1991; ELLENBERG, 1992; PRIMACK, 1993). Furthermore, many species tolerate only a limited level of human disturbances of their habitats (VAN SWAAY & WARREN, 1999; SWENGEL & SWENGEL, 1999; KITAHARA et al., 2000). This is of special relevance for Central European landscapes where human land-use for several hundreds or even thousands of years replaced the great majority of natural habitats.

However, many of the newly evolved Central European habitats that were extensively managed by men are even richer in species than the natural habitats such as calcareous grasslands (BOURN & THOMAS, 2002; POSCHLOD & WALLISDEVRIES, 2002; VAN SWAAY, 2002; WALLISDEVRIES et al., 2002). On the contrary, the intensively managed landscape evolving during the last few decades is rather impoverished in species if compared to extensively managed habitats (THOMAS 1983, 1984, 1991; ERHARDT, 1985a; KITAHARA & FUJII, 1994; THOMAS & MORRIS, 1994; KITAHARA et al., 2000; LÉON–CORTÉS et al., 1999, 2000; KITAHARA & SEI, 2001).

Butterflies and burnet moths (Lepidoptera: Papilionoidea, Hesperiidae, Zygaenidae) are an important umbrella species group for ecological evaluations on local, regional and interregional scales (e.g. THOMAS, 1984; POLLARD & YATES, 1993; LAUNER & MURPHY, 1994; THOMAS & MORRIS, 1994; SWENGEL & SWENGEL, 1999; WETTSTEIN & SCHMID, 1999; SMART et al., 2000). These insects are very sensitive bio-indicators due to their often highly complex life cycles (EBERT & RENNWALD, 1991; THOMAS, 1991; AKINO et al., 1999; BOUGHTON, 1999; VAN DYCK et al., 2000; HANSKI, 2001; THOMAS & ELMES, 2001; THOMAS et al., 2001). The distribution of many species is rather restricted (VAN SWAAY & WARREN, 1999; KUDRNA, 2002) and a lot of butterfly and burnet moth species are hardly found outside protected areas (e.g. nature reserves). Due to their higher attractiveness to researchers, these habitats are by far more intensively studied than the less speciesrich majority of the landscape. Therefore, it is necessary to accumulate more data about nontarget areas for nature-conservation measurements, and to analyse the ecological values and interactions between their different habitat types. This is of enhanced importance because protected areas occupy only a very limited part of the earth's surface. Therefore, understanding and management of the vast areas outside nature reserves is a key necessity for the conservation of biodiversity on a major scale.

In this study, the butterfly and burnet moth assemblages were analysed at 38 different habitat patches in the "Oettinger Forst" (Southern Germany) to address the following questions: (1) Are butterflies unequally distributed in the study area? (2) Are the butterfly assemblages of the studied forests less diverse than of the wind blows, mulched meadows and fertilised hay meadows? (3) Are man-made meadows significantly different from successional wind blows? (4) Are fertilised hay meadows less suitable for butterflies and burnet moths than unfertilised mulched meadows? (5) Are old quarries and sandpits important for the conservation of butterflies?

Material and methods

The "Oettinger Forst" in western Bavaria (southern Germany) was selected as study area. This mostly forested area extends as a strip of circa ten kilometres length along a mountain ridge that is the northern boundary of the "Nördliner Ries". As the altitude in the study area does not exceed 500 m the area has a hilly character. The northern part of the study area is part of the governmental unit of Mittelfranken, and the southern part belongs to Schwaben. The 49th latitude runs through the investigated area.

Forestry has a long tradition in the area and forests extend over more than 80 % of the surface. At least 50 % of these forests are spruce forests. Semi-natural deciduous forests of beech, oak and, at wet places, alder grow on less than 25 % of the surface. There are a lot of meadows: hay meadows, for agriculture and hunting; and mulched meadows (i.e. the grasses and herbs are cut into small pieces (but not removed afterwards) as hunting places —constituting less than 5 % within the forests, but abundant around the forested area. There are also some old guarries and sandpits whose surface may be 1 ‰ of the total area. The meadows were mowed once (partly twice) a year; mowing took place in early summer and, if twice a year, in late spring and late summer. Mulching took place in the second half of summer, mostly in the second half of July. As a result of the strong storms during the last decade, many large clearings in different successional stages exist throughout, maybe representing 10 % to 15 % of the study area. Small swamps often border the numerous traditionally-managed fishponds, but represent considerably less than 1% of the area.

Thirty-eight study plots representing the diversity of the different habitats present were equally distributed over the study area. They included planted coniferous, deciduous and mixed forests, clearings in early and medium successional stages, hay meadows and mulched meadows partly with small fields for game animals and small unmown areas, one swampy unmown maybe natural meadow, one quarry presently in use and two old quarries plus one old sandpit. An overview of the studied patches is given in Appendix 2.

All study patches were investigated during five different study periods during the year 2001 (22–

24 V; 13-15 VI; 4-6 VII; 23-24 VII; 29-30 VIII). Transect walks (slow walk, ca. two to three km per hour) were made for 20 minutes per patch per observation period; each butterfly and burnet moth seen within a radius of five meters was recorded. Hereby, a similarly large area (ca. 8,000 to 9,000 m²) of each surveyed patch was studied to achieve a maximum of comparability. Species which cannot be determined while flying were captured with a net and released again after determination. The number of observed individuals had to be estimated in the case of locally rather high densities (e.g. a great number of individuals at a small flowering thistle field). The recordings were performed when the weather was fine (temperature \geq 18°C, little wind, sunny). Observations were made between 10:00 and 17:00 hours (sometimes until 18:00 if atmospheric conditions permitted) so that daytime was neither too early nor too late for intensive butterfly activity.

The absolute numbers of observed individuals of butterflies and burnet moths are subject to several factors (e.g. butterfly activity is not constant for all species over the favoured daily flight period, even short cloudy periods have negative impacts on butterfly activity, traceability is not equal for all habitats (e.g. forests and meadows) and depends on vegetation height and density) (cf. POLLARD & YATES, 1993). Therefore, incidence (i.e. presence–absence data) was used for analyses of single species.

Diversity indices were calculated using BioDiversity Professional Beta (LAMBSHEAD et al., 1997). The Shannon indices H_s were calculated on the basis of \log_{10} . Eveness E_s was based on these \log_{10} Shannon indices. The dispersal ability of the species was rated using the classification of BINK (1992). Bink's nine dispersal classes were concentrated into three groups: poor (class 1 to 3), medium (class 4 and 5), and good dispersers (class 6 to 9).

Cluster analyses were performed using the UPGMA method. Euclidean distances calculated on single linkage were used. Principal component analysis was done using the varimax factor rotation method. For these two latter analyses, the packet STATISTICA (Stat Soft inc., 1993) was used. As input data for these two analyses, the following data sets were applied (i) presenceabsence data, (ii) the frequency of absolute incidences during the five investigation periods and (iii) the number of observed individuals per patch. The cluster analyses were performed (i) for all species observed and (ii) exclusively for the "common species" (i.e. at least 20 individuals observed during the whole observation period). PCA was done for all observed species including (i) all studied patches, (ii) all studied patches apart from the forested habitats (iii) all wind blows and (iv) all meadows.

Differences between means of numbers of individuals and species, means of incidences and means of diversity and dispersal indices were tested for significance by U-tests and Kruskal-Wallis ANOVAs for two-tailed tests and by Wilcoxon-tests for pair-wise tests using STATISTICA (Stat Soft inc., 1993). Tests for differences between means of incidences were calculated on the base of the "common species" (i.e. at least 20 individuals observed); "rare species" (i.e. less than 20 individuals observed) were excluded.

The nomenclature of KARSHOLT & RAZOWSKI (1996) was used. In the field, it is not possible to distinguish between *L. sinapis* and *L. reali* or between *Z. purpuralis* and *Z. minos*. These two sibling species complexes were therefore treated as two morpho–species for the analysis.

Results

A total of 42 butterfly and four burnet moth species were recorded for the 38 study patches, representing a total of around 5,000 individuals (see Appendix 1). Of these species, 13 were listed in the Red Data Book of Bavaria (GEYER & BÜCKER, 1992; WOLF, 1992) and 19 in the Red Data Book of Germany (PRETSCHER, 1998), but none in the European Red Data Book (VAN SWAAY & WARREN, 1999).

The butterflies were not equally distributed over the study patches. Focusing on the 25 "common species" (those with at least 20 individuals observed), only four species were more or less equally distributed (A. cardamines, G. rhamni, L. sinapis/reali, A. hyperantus), and occurred at any single patch at less than 10 % of the total number of individuals. On the other hand, seven species (P. brassicae, C. minimus, V. cardui, B. selene, M. galathea, P. aegeria, P. malvae) concentrated more than 20 % of all individuals observed at one single patch. The most extreme cases were B. selene and C. minimus with 63.3 % and 78.8 %, respectively, at their best patch. Furthermore, some of the "rare species" (with less than 20 individuals observed) appeared to occur accumulated (P. machaon 27.8 % of the 18 individuals at the best patch, A. urticae 29.4 % of the 17 individuals, B. dia 61.5 % of the 13 individuals, Z. viciae 23.5 % of the 17 individuals).

Poorly dispersing species were found on average in fewer patches than the medium dispersers, which were found in fewer patches than the good dispersers (10.3 \pm 10.2 SD, 15.9 \pm 12.5 SD, 20.8 \pm 9.4 SD, respectively); however, these differences were only marginally significant (Kruskal–Wallis ANOVA: p = 0.10).

The Shannon indices H_s ranged from 0.29 in the coniferous forest F1 to 1.25 in the wind blow C8 (mean: 0.92 ± 0.21 SD). The Eveness E_s ranged from 0.60 in the deciduous forest F5 to 0.95 in the coniferous forest F1 (mean: 0.78 ± 0.08 SD).

The hypothesis of question 1 can therefore be accepted. The unequal distribution of butterflies and burnet moths in the study area is the necessary pre-requisite to address the other four questions.

Forest versus non-forest

The mean number of butterfly and burnet moth species was significantly lower in forest patches than in non-forest patches (6.7 \pm 2.4 SD, 18.8 ± 4.6 SD, respectively, *U*-test: *p* = 0.0002). A similar result was obtained for the mean number of observed individuals (44 ± 23 SD, 178 ± 155 SD, respectively, U-test: p = 0.0015). Also the Shannon indices were significantly lower in the forest than in non-forest patches (H_s : 0.58 ± 0.18 SD, 0.99 ± 0.14 SD, respectively, *U*-test: p = 0.0002), but there was no significant difference between the means of the Eveness (E_s : 0.76 ± 0.14 SD, 0.78 ± 0.07 SD, respectively, *U*-test: p = 0.66). The patch with the lowest number of individuals was the sole analysed spruce forest F1 where only eleven butterflies belonging to two species were observed during the five visits. In this patch, the lowest Shannon index (H_s: 0.29) and the highest Eveness (E_s: 0.95) were calculated. The mean incidences of the 25 common species differed significantly between forest and non-forest habitats (0.46 ± 0.83 SD, 1.11 ± 0.71 SD, respectively, Wilcoxon-test: p = 0.0002). A total of 14 of these species showed significant differences (U-tests: p < 0.05): 13 were more common in non-forest patches and only one was more common in forested patches (i.e. P. aegeria). The results for five of these species were significant after Bonferroni correction (L. sinapis / reali, A. levana, A. adippe, P. aegeria, O. sylvanus).

All cluster analyses performed yielded more or less similar results: the investigated forest patches clustered mostly closely together whereas all other patches showed considerably greater differentiations of their butterfly and burnet moths species assemblages, but no reliable differentiation between the different habitat types was found (fig. 1). Furthermore, all principal component analyses separated the forested habitats clearly from the other patches (fig. 2A).

Meadows versus successional patches

The non-forest patches can be distinguished into meadows (mown or mulched, in some cases with small fields for game animals) and patches in the process of natural succession (forest clearings, fallow meadows, old and present quarries, old sandpits). The windblows - these clearings were by far the most common successional habitat type of the study area— had a rather similar mean number of individuals as the meadows (185 ± 245 SD, 187 ± 82 SD, respectively, U-test: p = 0.14). However, the mean Shannon indices and Eveness were significantly higher in the wind blows than in the meadows ($H_{\rm s}$: 1.04 ± 0.11 SD, 0.90 ± 0.15 SD, respectively, U-test: p = 0.027; E_s: 0.82 ± 0.06 , 0.73 ± 0.06 , respectively, U-test: p = 0.0031). Furthermore, the mean number of species trended to be higher in clearings $(19.4 \pm 4.3 \text{ SD}, 18.1 \pm 5.7 \text{ SD}, \text{ respectively}, U-\text{test:}$ p = 0.76). The mean incidences of the 25 common species did not show a distinct distribution pattern (1.06 ± 0.70 SD, 1.09 ± 0.78 SD, respectively, Wilcoxon-test: p = 0.89), but the incidences of three individual species differed in different habitat types: *M. galathea* was significantly more often observed in clearings (*U*-test: p = 0.031) whereas *M. jurtina* and *P. c-album* occurred more frequently in meadows (*U*-test: p = 0.026 and 0.0007, respectively). After Bonferroni correction, only the difference for the third species was significant.

Principal component analyses revealed that the windblows were much more alike than the meadows. With few exceptions, the windblows were nested within the variance breadth of the meadows (fig. 2B). Within the windblows, the eight of early successional stages had a much broader intervariance than the four of later succession (fig. 2C).

Hay meadows versus mulched meadows

In hay meadows, the mean numbers of observed individuals were about 49.7 % higher than in mulched meadows; nevertheless, this difference was not significant (214 \pm 63 SD, 143 \pm 88 SD, respectively, U-test: p = 0.17). The mean number of species also trended to be higher in hay meadows than in mulched meadows $(19.8 \pm 5.9 \text{ SD})$, 14.8 \pm 5.8 SD, respectively, U-test: p = 0.22). The mean incidences of the 25 common species were significantly higher in the hay meadows (1.19 ± 0.96, 0.78 ± 0.68, respectively, Wilcoxontest: p = 0.0069), and the incidence of two species differed significantly conforming to the meadow type: P. rapae and P. c-album had higher incidences in mowed meadows (U-test: p = 0.053and 0.020, respectively), but these were not significant after Bonferroni correction. Principal component analyses supported a weak difference between mulched and fertilised hay meadows, as these were somewhat separated, but there was a great overlap of their variance components (fig. 2D). However, mean Shannon indices and Eveness were similar for the hay and mulched meadows (H_c : 0.91 ± 0.18, 0.83 ± 0.09, respectively, *U*-test: p = 0.33; $E_s: 0.70 \pm 0.07$, 0.73 ± 0.06 , respectively, *U*-test: p = 0.46).

Old quarries and sandpits

The two old quarries and the old sandpit represent man-made successional habitats with intensive human disturbance in the past. They differ somewhat from all the other investigated habitats in the UPGMA analysis (fig. 1), but were nested within the variance breadth of the meadows in the principal component analyses (fig. 2B).

These three patches trended to a lower mean of observed individuals (150 \pm 41 SD) than the non-anthropogenic successional habitats (i.e. windblows: 185 \pm 245 SD); nevertheless, this difference was not significant (*U*-test: p = 0.39). On



Fig. 1. UPGMA cluster diagram of the differentiation of the butterfly and burnet moth assemblages of the 38 patches using euclidean distances calculated from presence–absence data of all 46 recorded species.

Fig. 1. Diagrama de agrupamiento UPGMA referente a la diferenciación de las concentraciones de mariposas diurnas y zygenas en las 38 parcelas utilizando distancias euclidianas calculadas conforme a los datos de presencia / ausencia de las 46 especies identificadas.

the contrary, the mean number of species trended to be higher in the two old guarries and the old sandpit than in the clearings (22.0 \pm 0.0 SD, 19.3 \pm 5.0 SD, respectively, *U*-test: *p* = 0.27). Focusing on the individual species, their mean incidences differed significantly between these two habitat types with higher mean incidences in the quarries and the sandpit than in the clearings $(1.33 \pm 0.88 \text{ SD}, 1.09 \pm 0.70 \text{ SD}, \text{ respectively},$ Wilcoxon-test: p = 0.041). Four of the 25 common species (L. sinapis / reali, C. minimus, P. calbum, P. aegeria) trended to significantly higher incidences in the guarries and sandpits than in the clearings (U-tests: p < 0.05), but this was not significant after Bonferroni correction; opposite results were not observed. Of these four species, C. minimus occurred exclusively in the two old quarries, where it was even common. The two single observed individuals of C. rubi and M. athalia were found in the old sandpit. Furthermore, the rare species Z. purpuralis / minos and Z. trifolii were not found in clearings. Mean Shannon indices and Eveness were marginally significantly higher in the old quarries and the sandpit than in the windblows (H_s : 1.17 ± 0.04, 1.04 ± 0.11, respectively, U-test: p = 0.051; E_s : 0.87 ± 0.03, 0.81 ± 0.06 , respectively, *U*-test: p = 0.083).

Comparing the old quarries and the sandpit not only with the clearings but with all nonforest patches analysed, quite similar results were obtained, but the statistical support was stronger. Thus, mean Shannon indices and Eveness were significantly higher even after Bonferroni correction in the old quarries and the sandpit than in all the other non-forest patches (H_s : 1.17 ± 0.04, 0.97 ± 0.10, respectively, *U*-test: p = 0.012; E_s : 0.87 ± 0.03, 0.77 ± 0.07, respectively, *U*-test: p = 0.016). In the comparison with all non-forest patches, the difference of mean incidences of *C. minimus* was significant even after Bonferroni correction (*U*-test: p < 0.0001).

Discussion

Most butterflies and burnet moth species observed are unequally distributed in the "Oettinger Forst". This is a frequently observed phenomenon for butterflies (e.g. BOUGHTON, 1999; DENNIS & HARDY, 1999; COWLEY et al., 2000, 2001; GUTIÉRREZ et al., 2001). One important factor is the existence of rather different habitat types, each of which has a great variety of carrying capacities for individual species (i.e. one habitat can be an optimum habitat for one species and unsuitable for another species) (THOMAS et al., 2001). Thus, a landscape can harbour different metapopulation structures for different species and species groups (HANSKI, 1999). The resulting structure is strongly influenced by patch size (e.g. THOMAS et al., 1992; HANSKI, 1994; WETTSTEIN & SCHMID, 1999; SUMMERVILLE & CRIST, 2001), patch quality (e.g. LEÓN–CORTÉS et al., 1999; THOMAS et al., 2001) and connectivity of patches (e.g. WETTSTEIN & SCHMID, 1999; HADDAD, 2000; THOMAS et al., 2001). Especially for the latter, the dispersal ability of the different species is of great importance. Consequently, good dispersing species had a wider distribution in our study area than the medium dispersers, and poor dispersing species had the most restricted distribution.

Fewer butterflies in forests

The contrast between forest and non-forest patches was the most important factor for the unequal distribution of the species. This also answers question 2: the forests investigated were much poorer habitats for the great majority of butterfly species than the windblows and meadows: incidences, number of species and individuals as well as Shannon indices were significantly lower in forests than in non-forests. This might be largely due to a very reduced spectrum of flowers as nectar sources and due to strongly reduced insolation of potential larval habitats.

Similar results are known from other parts of the temperate zone of the northern hemisphere (e.g. ERHARDT, 1985b; KITAHARA & WATANABE, 2001). Only one of the common species (i.e. *P. aegeria*) clearly preferred forests as habitat. The ecological demand of this species has been known for a long time and is well documented (WEIDEMANN, 1986; EBERT & RENNWALD, 1991; HILL et al., 1999; ASHER et al., 2001). The deciduous and mixed forests were generally richer in butterflies than the planted coniferous forest studied. This seems to be a more general feature as the same phenomenon has been observed elsewhere, such as in Japan (KITAHARA, 1999, 2000).

Windblows have higher butterfly diversity than meadows

Windblows had higher Shannon indices than meadows and showed a trend for higher species numbers. Some species of the German Red Data Book (PRETSCHER, 1998) had strong populations exclusively in the clearings (i.e. *B. dia, B. selene*) whereas none of the Red Data Book species was frequent in the meadows. The two mentioned *Boloria* species are typical of sunny forest edges; especially *B. dia* is characteristic for thermophilous southern slopes in the process of succession (EBERT & RENNWALD, 1991; SETTELE et al., 1999).

This answers question 3: windblows and meadows differ considerably. This is further supported by the principal component analyses, which revealed some weak diversification between these two habitat types. The clearings seem to offer a sufficient amount of habitat necessary to support the survival of most of the species of the non-forest habitats observed in the study area. The relatively high ecological value of these patches might be due to the relatively high



Fig. 2. Principal Component Analyses of the species compositions (presence / absence data) of: A. All 38 studied patches (the first component explains 32.1 %, the second 19.6 % of the total variance); B. The 32 non-forest patches (the first component explains 30.8 %, the second 22.4 % of the total variance); C. The 13 *windblows* (the first component explains 36.9 %, the second 24.0 % of the total variance); D. The 15 meadows (the first component explains 31.6 %, the second 26.1 % of the total variance). Abbreviations: \Box Forest; + . *Windblow* (in figure 2C: + . Early succession; %. Medium succession; \oplus . Others);) . Meadow (in figure 2D: # . Hay meadow;) . Mulched meadow; (. Other meadows, sometimes fallow); *****. Quarry; **+**. Sand pit.

Fig. 2. Análisis de Componentes Principales de la composición de especies (datos de presencia l ausencia) de: A. Las 38 parcelas estudiadas (el primer factor es responsable del 32,1 % de la variación total y el segundo del 19,6 %); B. Las 32 parcelas sin masa forestal (el primer factor es responsable del 30,8 % de la variación total y el segundo del 22,4 %); C. Los 13 windblows (el primer factor es responsable del 36,9 % de la variación total y el segundo del 24,0 %); D. Los 15 prados (el primer factor es responsable del 31,6 % de la variación total y el segundo del 26,1 %). Abreviaturas: \Box . Zonas boscosas; + . Windblows (en la figura 2C: + . Sucesión temprana; %. Sucesión media; \oplus . Otros);) . Prado (en la figura 2D: # . Prado de heno;) . Prado cubierto de paja; (. Otro tipo de prado, a veces tierras en barbecho); ★. Cantera; ✦. Arenal.

amount of attractive nectar sources for butterflies and burnet moths such as thistle fields (especially composed of *Cirsium arvense*) and due to the fact that the flowering vegetation was not removed once or twice a year. Thus, human impact on these patches was less than on most of the meadows.

The other non-forest habitats of the study area maintained by agricultural and hunting activities seemed to be no stimulus for further increases of biodiversity of butterflies and burnet moths. This cannot be explained simply by a generally reduced biodiversity in managed grassland in comparison to successional patches (FRAZER, 1965; SOUTHWOOD & VAN EMDEN, 1967; DEMPSTER, 1971; ERHARDT, 1985a). It is more likely due to the manner and intensity of grassland management. The hay meadows were fertilised so that they were relatively rich in soil nutrients, especially nitrogen. The mulched meadows were also rich in nitrogen as the hay was not removed from these patches so that nitrogen could accumulate. In general, eutrophication changes the plant composition and decreases their species numbers (e.g. NEITZKE, 1991; KAHMEN et al., 2002). While the number of invertebrate species correlates to the number of plant species (cf. STEFFAN-DEWENTER & TSCHARNTKE, 2002), as was also demonstrated for butterflies (STEFFAN-DEWENTER & TSCHARNTKE, 2000), a great number of lepidopterans react negatively and rather sensitively to the eutrophication of their habitats (ERHARDT, 1985a; DENNIS, 1992; SCHMITT, 1993; Oostermijer & Van Swaay, 1998; Van es et al., 1998; FISCHER & FIEDLER, 2000). Thus, the enhanced soil-nitrogen values of the fertilised and mulched meadows might explain their relatively low attractiveness for butterflies and burnet moths.

Mowing or mulching?

The unfertilised mulched meadows were less suitable for butterflies and burnet moths than the fertilised hay meadows. The fertilised hay meadows trended to higher numbers of species and individuals, and the mean incidence of the 25 common species was higher, so that question 4, in general, has to be negated for the study area. Principal component analyses also revealed some weak diversification between these two types of meadows. This shows that mulching as performed in the study area in late summer is not enhancing lepidopteran biodiversity in comparison to traditionally managed hay meadows with fertilisation and one (sometimes two) cuts a year. However, there is evidence that mulching twice a year or early in summer reduces soil nitrogen (NEITZKE, 1991; KAHMEN et al., 2002; WALLISDEVRIES et al., 2002) so that in some special cases even this method might be an acceptable tool for conservation measures of meadows.

Of conservation interest: old quarries and sandpits

The two old quarries and the old sandpit had significantly higher incidences of butterflies and burnet moth species than the other successional patches (i.e. windblows), and Shannon indices and Eveness were significantly higher than in the other non-forest patches. Besides, the number of species trended to be higher in these patches, and three species of the German Red Data Book (PRETSCHER, 1998) (i.e. C. minimus, C. rubi, M. athalia) were only observed in these patches. This positive answer to question 5 underlines the importance of such structures for the conservation of the local biodiversity in a non-target area. Furthermore, such habitats might play a role as stepping-stones in the regional gene flow, especially for poor dispersers like C. minimus (BAGUETTE et al., 2000; COWLEY et al., 2001). This latter species depended completely on these two old quarries as its single larval foodplant Anthyllis vulneraria only grew in these two places in the study area.

The quarries and the sandpit had formerly been rather strongly modified by human activities. Since their human abandonment, barren flower-rich swards and thistle fields have developed on the exposed nutrient-poor soils. There is thus the somewhat paradoxical situation that the patches with most intensive human disturbance in the past have now developed, since abandonment, a habitat type that is typical of low human disturbance. At present, these quarries and sandpits are definitively less disturbed by human activities than the mown and mulched meadows, so that these three patches might be functionally similar to unimproved grassland. If we accept this hypothesis, than we can postulate that the higher the degree of human disturbance, the lower the diversity of butterflies and burnet moths in non-forested habitats in the study area. This is a frequently observed phenomenon in a number of other investigations around the world (YAMAMOTO, 1977; RUSZCZYK & DEARAUJO, 1992; KITAHARA & FUJII, 1994; HILL et al., 1995; KITAHARA et al., 2000; KITAHARA & SEI, 2001).

Acknowledgements

I thank the Game Conservancy Deutsch-land and Fürst Oettingen-Spielberg (Oettingen, Germany) for the financial and logistical support that made this investigation possible. Thanks too to Andreas Erhardt (Basel, Switzerland), Masahiko Kitahara (Kenmarubi, Japan), Mechthild Neitzke (Trier, Germany), László Rákosy (Cluj, Romania), Zoltán Varga (Debrecen, Hungary) and two anonymous referees for useful comments on a draft version of this article and Desmond Kime (Linkebeek, Belgium) for the correction of my English.

References

- AKINO, T., KNAPP, J. J., THOMAS, J. A. & ELMES, G. W., 1999. Chemical mimicry and host specificity in the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. *Proceedings of the Royal Society of London B*, 266: 1419–1426.
- ASHER, J., WARREN, M., FOX, R., HARDING, P., JEFFCOATE, G. & JEFFCOATE, S., 2001. The millennium atlas of butterflies in Britain and Ireland. Oxford University Press, Oxford.
- BAGUETTE, M., PETIT, S. & QUÉVA, F., 2000. Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. *Journal* of Applied Ecology, 37: 100–108.
- BINK, F. A., 1992. Ecologische Atlas van de Dagvlinders van Noordwest-Europa. Schuyt & Co. Uitgevers en Importeurs, Haarlem.
- BOUGHTON, D. A., 1999. Empirical evidence for complexe source–sink dynamics with alternative states in a butterfly metapopulation. *Ecology*, 80: 2727–2739.
- BOURN, N. A. D. & THOMAS, J. A., 2002. The challenge of conserving grassland insects at the margins of their range in Europe. *Biological Conservation*, 104: 285–292.
- COWLEY, M. J. R., THOMAS, C. D., ROY, D. B., WILSON, R. J., LÉON–CORTÉS, J. L., GUITIÉRREZ, D., BULMAN, C. R., QUINN, R. M., MOSS, D. & GASTZZON, K. J., 2001. Density–distribution relationships in British butterflies. I. The effect of mobility and spatial scale. *Journal of Animal Ecology*, 70: 410–425.
- COWLEY, M. J. R., WILSON, R. J., LEÓN–CORTÉS, J. L., GUTIÉRREZ, D., BULMAN, C. R. & THOMAS, C. D., 2000. Habitat–based statistical models for predicting the spatial distribution of butterflies and day–flying moths in a fragmented landscape. Journal of Applied Ecology, 37: 60–72.
- DEMPSTER, J. P., 1971. Some effects of grazing on the population ecology of the Cinnabar Moth (*Thyria jacobaeae* L.). *Symposium of the British Ecological Society*, 11: 517–526.
- DENNIS, R. L. H., 1992. *The ecology of butterflies* in Britain. Oxford Science Publications, Oxford.
- DENNIS, R. L. H. & HARDY, P. B., 1999. Targeting squares for survey: predicting species richness and incidence of species for a butterfly atlas. *Global Ecology and Biogeography*, 8: 443–454.
- EBERT, G. & RENNWALD, E. (Eds.), 1991. *Die Schmetterlinge Baden-Württembergs*, Volume 1 and 2. Verlag Eugen Ulmer, Stuttgart.
- ELLENBERG, H., 1992. Zeigerwerte der Gefäßpflanzen Mitteleuropas (3rd ed.). Scripta Geobotanica, Verlag Erich Göltze, Göttingen.
- ERHARDT, A., 1985a. Day–active Lepidoptera: sensitive indicators of cultivated and abandoned grassland. *Journal of Applied Ecology*, 22: 849–861.
- 1985b. Wiesen und Brachland als Lebensraum für Schmetterlinge: eine Fallstudie in Tavetsch (GR). Birkhäuser, Basel.

- FISCHER, K. & FIEDLER, K., 2000. Response of the copper butterfly *Lycaena tityrus* to increased leaf nitrogen in natural food plants: ecidence against the nitrogen limitation hypothesis. *Oecologia*, 124: 235–241.
- FRAZER, J. F. D., 1965. Butterflies of chalk grassland: A conservation problem. Proceedings of the 12th international Congress of Entomology, London 8–16 July 1964, 355.
- GEYER, A. & BÜCKER, M., 1992. Rote Liste gefährdeter Tagfalter (Rhopalocera) Bayerns. In: Beiträge zum Artenschutz 15 Rote Liste der gefährdeten Tiere Bayerns: 206–213 (Bayerisches Landesamt für Umweltschutz, Ed.). Schriftenreihe des Bayerischen Landesamtes für Umweltschutz 111.
- GUTIÉRREZ, D., LÉON-CORTÉS, J. L., MENÉDEZ, R., WILSON, R. J., COWLEY, M. J. R. & THOMAS, C. D., 2001. Metapopulations of four lepidopteran herbivores on a single host plant, *Lotus corniculatus*. *Ecology*, 82: 1371–1386.
- HADDAD, N., 2000. Corridor length and patch colonization by a butterfly, *Junonia coenia*. *Conservation Biology*, 14: 738–745.
- HANSKI, I., 1994. Patch–occupancy dynamics in fragmented landscapes. *Trends in Ecology and Evolution*, 9: 131–135.
- 1999. Metapopulation ecology. Oxford University Press, Oxford.
- 2001. Spatially realistic theory of metapopulation ecology. *Naturwissenschaften*, 88: 372–381.
- HILL, J. K., HAMER, K. C., LACE, L. A. & BANHAM, W. M. T., 1995. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *Journal of Applied Ecology*, 32: 754–760.
- HILL, J. K., THOMAS, C. D. & HUNTLEY, B., 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society of London B*, 266: 1197–1206.
- KAHMEN, S., POSCHLOD, P. & SCHREIBER, K.–F., 2002. Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. *Biological Conservation*, 104: 319–328.
- KARSHOLT, O. & RAZOWSKI, J. (Eds.), 1996. *The Lepidoptera of Europe. A distributional checklist.* Apollo Books, Stenstrup.
- KITAHARA, M., 1999. Species diversity of butterfly communities in a variety of woodlands at the northern foot of Mt. Fuji, Central Japan. *Japanese Journal of Environmental Entomology and Zoology*, 10: 11–29.
- 2000. Food resource useage of adult butterfly communities in woodland habitats at the northern foot of Mt. Fuji, Central Japan. Japanese Journal of Environmental Entomology and Zoology, 11: 61–81.
- KITAHARA, M. & FUJII, K., 1994. Patterns in the structure of grassland butterfly communities along a gradient of human disturbance: further analysis based on the generalist/specialist

concept. *Research in Population Ecology*, 36: 187–199.

- KITAHARA, M. & SEI, K., 2001. A comparison of the diversity and structure of butterfly communites in semi–natural and human–modified grassland habitats at the foot of Mt. Fuji, central Japan. *Biodiversity and Conservation*; 10: 331–351.
- KITAHARA, M., SEI, K. & FUJII, K., 2000. Patterns in the structure of grassland butterfly communities along a gradient of human disturbance: further analysis based on the generalist/specialist concept. *Population Ecology*, 42: 135–144.
- KITAHARA, M. & WATANABE, M., 2001. Relationships of butterfly community diversity to vegetational species richness in and around the Aokigahara woodland at the northern foot of Mt. Fuji, Central Japan. Japanese Journal of Environmental Entomology and Zoology, 12: 131–145.
- KUDRNA, O., 2002. The distribution atlas of European butterflies. *Oedippus*, 20: 1–342.
- LAMBSHEAD, P. J. D., PATERSON, G. L. J. & GAGE, J. D., 1997. *BioDiversity Professional Beta*. The Natural History Museum & The Scottish Association for Marine Science.
- LAUNER, A. E. & MURPHY, D. D., 1994. Umbrella species and the conservation of habitat fragments: a case of a threatened butterfly and a vanishing grassland ecosystem. *Biological Conservation*, 69: 145–153.
- LEÓN-CORTÉS, J. L., COWLEY, M. J. R. & THOMAS, C. D., 1999. Detecting decline in a formerly widepread species: how common is the common blue butterfly *Polyommatus icarus*? *Ecography*, 22: 643–650.
- 2000. The distribution and decline of a widespread butterfly Lycaena phlaeas in a pastoral landscape. Ecological Entomology, 25: 285–294.
- NEITZKE, A., 1991. Vegetationsdynamik in Grünlandbrachesystemen. Arbeitsberichte Lehrstuhl Landschaftsökologie Münster, 13: 1–140.
- OOSTERMEIJER, J. G. B. & VAN SWAAY, C. A. M., 1998. The relationship between butterflies and environmental indicator values: a tool for conservation in a changing landscape. *Biological Conservation*, 86: 271–280.
- POLLARD, E. & YATES, T. J., 1993. Monitoring butterflies for ecology and conservation. The British Butterfly Monitoring Scheme. Chapman & Hall, London.
- POSCHLOD, P. & WALLISDEVRIES, M. F., 2002. The historical and socioeconomic perspective of calcareous grasslands —lessons from the distant and recent past. *Biological Conservation*, 104: 361–376.
- PRETSCHER, P., 1998. Rote Liste der Großschmetterlinge (Macrolepidoptera). In: Rote Liste gefährdeter Tiere Deutschlands: 87–111 (Bundesamt für Naturschutz, Ed.). Schriftenreihe für Landschaftspflege und Naturschutz 55.
- PRIMACK, R. B., 1993. *Essentials of conservation biology*. Sinauer Associates, Sunderland.

- RUSZCZYK, A. & DEARAUJO, A. M., 1992. Gradients in butterfly species diversity in an urban area in Brasil. *Journal of the Lepidopterists' Society*, 46: 255–264.
- SCHMITT, T., 1993. Biotopansprüche von *Erebia medusa brigobanna* FRUHSTORFER, 1917 (Rundaugen–Mohrenfalter) im Nordsaarland. *Atalanta*, 24: 33–56.
- SETTELE, J., FELDMANN, R. & REINHARDT, R., 1999. Die Tagfalter Deutschlands — Ein Handbuch für Freilandökologen, Umweltplaner und Naturschützer. Ulmer, Stuttgart.
- SMART, S. M., FIRBANK, L. G., BUNCE, R. G. H. & WATKINS, J. W., 2000. Quantifying changes in abudance of food plants for butterfly larvae and farmland birds. *Journal of Applied Ecol*ogy, 37: 398–414.
- SOUTHWOOD, T. R. E. & VAN EMDEN, H. F., 1967. A comparison of the fauna of cut and uncut grassland. *Zeitschrift für angewandte Entomologie*, 60: 188–198.
- STEFFAN–DEWENTER, I. & TSCHARNTKE, T., 2000. Butterfly community structure in fragmented habitats. *Ecology Letters*, 3: 449–456.
- 2002. Insect communities and biotic interactions on fragmented calcareous grasslands —a mini review. *Biological Conservation*, 104: 275–284.
- SUMMERVILLE, K. S. & CRIST, T. O., 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera). *Ecology*, 82: 1360–1370.
- SWENGEL, S. R. & SWENGEL, A. B., 1999. Correlations in abundance of grassland songbirds and prairie butterflies. *Biological Conservation*, 90: 1–11.
- THOMAS, C. D., THOMAS, J. A. & WARREN, M. S., 1992. Distribution of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia*, 92: 563–567.
- THOMAS, J. A., 1983. The ecology and conservation of Lysandra bellargus (Lepidoptera: Lycaenidae) in Britain. Journal of Applied Ecology, 20: 59–83.
- 1984. The conservation of butterflies in temperate countries: past efforts and lessons for the future. In: *Biology of butterflies*: 333–353 (R. I. Vane–Wright & P. Ackery, Eds.). Academic Press, London.
- 1991. Rare species conservation: case studies of European butterflies. In: *The scientific management of temperate communities for conservation*: 149–197 (I. Spellerberg, B. Goldsmith & M. G. Morris, Eds.). Blackwell, Oxford.
- THOMAS, J. A. & ELMES, G. W., 2001. Food-plant niche selection rather than the presence of ant nests explains oviposition patterns in the myrmecophilous butterfly genus *Maculinea*. *Proceedings of the Royal Society of London B*, 268: 471–477.
- THOMAS, J. A. & MORRIS, M. G., 1994. Patterns, mechanisms and rates of decline among UK invertebrates. *Philosophical Transactions of the Royal Society of London B*, 344: 47–54.
- THOMAS, J. A., BOURN, N. A. D., CLARKE, R. T.,

STEWART, K. E., SIMCOX, D. J., PEARMAN, G. S., CURTIS, R. & GOODGER, B., 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society of London B*, 268: 1791–1796.

- VAN DYCK, H., OOSTERMEIJER, J. G. B., TALLOEN, W., FEENSTRA, V., VAN DER HIDDE, A. & WYNHOFF, I., 2000. Does the presence of ant nests matter for oviposition to a specialized myrmecophilous *Maculinea* butterfly? *Proceedings of the Royal Society of London B*, 267: 861–866.
- VAN ES, J., PAILLISSON, J.–M. & BUREL, F., 1998. Impacts de l'eutrophisation de la végétation des zone humide de fonds de vallées sur la biodiversité des rhopalocères (Lepidoptera). *Vie et Milieu*, 49: 107–116.
- VAN SWAAY, C. A. M., 2002. The importance of calcareous grasslands for butterflies in Europe. *Biological Conservation*, 104: 315–318.
- VAN SWAAY, C. A. M. & WARREN, M., 1999. *Red Data Book of European butterflies (Rhopa-locera)*. Nature and environment 99, Council

of Europe Publishing, Strasbourg.

- WALLISDEVRIES, M. F., POSCHLOD, P. & WILLEMS, J. H., 2002. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation*, 104: 265–273.
- WEIDEMANN, H.-J., 1986. *Tagfalter*. Volume 1. Verlag J. Neumann–Neudamm, Melsungen.
- WETTSTEIN, W. & SCHMID, B., 1999. Conservation of arthropod diverstiy in montane wetland: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. Journal of Applied Ecology, 36: 363–373.
- WOLF, W., 1992. Rote Liste gefährdeter Nachtfalter Bayerns. In: Beiträge zum Artenschutz 15 Rote Liste der gefährdeten Tiere Bayerns: 214–236 (Bayerisches Landesamt für Umweltschutz, Ed.). Schriftenreihe des Bayerischen Landesamtes für Umweltschutz 111.
- YAMAMOTO, M., 1977. A comparison of butterfly assemblages in and near Sapporo city, northern Japan. Journal of the Faculty of Sciences of Hokkaido University, Series 6 Zoology, 20: 621–646.

Appendix 1. Shannon index, Eveness and number of observed butterflies and burnet moth for all species and patches investigated in the "Oettinger Forst" (Bavaria, Germany) during the five investigation periods in 2001: RDB. Red Data Book [of Germany (G) (PRETSCHER, 1998); of Bavaria (BY) (GEYER & BÜCKER, 1992; WOLF, 1992); Endangered (3); Prewarning list (V)]; T. Total number of observed individuals; P. Total number of inhabited patches.

	R	DB					Forests	;
	G	BY	Т	Ρ	F1	F2	F3	F4
Shannon index H _c					0.285	0.785	0.684	0.676
Eveness E					0.947	0.869	0.757	0.749
Pyrgus malvae (L., 1758)			51	16	-	-	-	-
Carterocephalus palaemon (Pall., 1771)	V		80	23	-	1	3	4
Thymelicus lineola (O 1808)			9	5	-	-	-	-
Thymelicus sylvestris (Poda 1771)			180	23	-	-	_	-
Ochlodes sylvanus (Esp. [1778])			362	34	-	4	1	-
Panilio machaon 1 1758	V	V	18	14	-	-	-	-
Lentidea sinanis (l. 1758)/reali Reissinger 1989	v	v	111	28		_		
Anthocharis cardamines (I 1758)	•		103	27				4
Pieris brassicae (l. 1758)			23	13		_		
$\frac{1}{1} \frac{1}{1} \frac{1}$			136	20				
$\frac{\text{Pieris Tapae}(L, 1756)}{\text{Dioris papi}(L, 1758)}$			042	20	-	-	-	-
Collies hyple (L., 1758)		<u></u>	943	30	4	19	12	
Collas nyale (L., 1758)		V	3	2	-	-	-	-
Gonepteryx rnamni (L., 1758)			270	30	-	12	2	3
Lycaena phiaeas (L., 1761)			13	10	-	-	-	-
Callophrys rubi (L., 1758)	<u>v</u>		1	1	-	-	-	-
Cupido minimus (Fuessly, 1775)	V	V	33	2	-	-	-	-
Celastrina argiolus (L., 1758)			11	8	-	-	-	-
Aricia agestis ([Den. & Schiff.], 1775)	V	V	1	1	-	-	-	-
Polyommatus icarus (Rott., 1775)			42	16	-	-	-	-
Argynnis paphia (L., 1758)			48	19	-	3	-	1
Argynnis adippe ([Den. & Schiff.], 1775)	3	3	60	24	-	-	-	-
Issoria lathonia (L., 1758)			3	3	-	-	-	-
Brenthis ino (Rott., 1775)	V	3	2	1	-	-	-	-
Boloria euphrosyne (L., 1758)	3	V	2	2	-	-	-	-
Boloria selene ([Den. & Schiff.], 1775)	V		98	9	-	-	-	-
Boloria dia (L., 1758)	3	V	13	4	-	-	-	-
Vanessa atalanta (L., 1758)			44	25	-	-	2	1
Vanessa cardui (L., 1758)			38	19	-	-	-	-
Inachis io (L., 1758)			465	31	-	7	1	-
Aglais urticae (L., 1758)			17	9	-	-	-	-
Polygonia c-album (L., 1758)			36	13	-	-	1	-
Araschnia levana (L., 1758)			276	30	-	-	-	-
Melitaea athalia (Rott., 1775)	3		1	1	-	-	-	-
Limenitis camilla (L., 1764)	3	V	4	2	-	-	-	-
Apatura ilia ([Den. & Schiff.], 1775)	3	3	1	1	-	-	-	-
Apatura iris (L., 1758)	V	3	2	2	-	-	-	-
Pararge aegeria (L., 1758)			158	28	7	13	1	8
Coenonympha arcania (L., 1761)	V		6	5	-	-	-	-
Coenonympha pamphilus (L., 1758)			71	14	-	-	-	-
Aphantopus hyperantus (L., 1758)			888	33	-	4	-	2
Maniola jurtina (L., 1758)			334	25	-	-	-	-
Melanargia galathea (L., 1758)			26	11	-	-	-	-
Zygaena purpuralis (Brünn., 1763)								
/minos ([Den. & Schiff.], 1775)	3	V	4	2	-	-	-	-
Zygaena viciae ([Den. & Schiff.], 1775)	V		17	8	-	-	-	-
Zygaena filipendulae (L., 1758)			8	4	-	-	-	-
Zygaena trifolii (Esp., 1783)	3	3	2	2	-	-	-	-
Total			5014		11	63	23	46

Apéndice 1. Índices de Shannon, Eveness y número total de mariposas diurnas y zygenas observado de la totalidad de las especies y parcelas estudiadas en "Oettinger Forst" (Baviera, Alemania) durante las cinco fases del estudio llevadas a cabo en 2001: RDB. Red Data Book [de Alemania (G) (PRETSCHER, 1998); de Baviera (BY) (GEYER & BÜCKER, 1992; WOLF, 1992); En peligro de extinción (3); Lista de preaviso (V)]; Total. Número total de especímenes observados; Patch. Número total de parcelas con poblaciones de especies.

For	ests	Windblows										
F5	F6	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11
0.540	0.480	1.089	0.981	0.873	1.039	1.133	0.911	1.062	1.252	1.150	0.950	1.034
0.598	0.617	0.837	0.815	0.696	0.883	0.844	0.875	0.846	0.865	0.804	0.730	0.808
-	-	2	-	-	3	1	-	1	12	2	2	6
-	-	-	1	2	-	-	-	-	1	6	-	-
-	-	-	3	1	-	-	-	-	3	-	-	-
-	-	10	-	7	1	1	-	16	24	4	1	1
_	-	5	7	37	3	2	9	12	12	36	13	7
_	-	-	1	-	-	-	1	1	-	1	1	
-	-	1	8	1	-	2	3	4	11	4	4	3
	1	2	1	-	1	4	6	1	9	2	3	3
	-	-	-	_	-	1	-	-	2	1	-	
		1				2		2	23	1		
10	2/	15	2	1	5	15	6		- 25	12	10	
	24	15	2	4		15	0	9	2	15	19	I
	-	-	-	-	-	-	-	-	16	-	-	- 11
I	4	2	1	0	9	2	2	9	10	1	2	1
-	-	-	-	-	-	2	-	-	1	I	I	I
-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	1	-	-	-	-	1	1	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	1	-	I	3		2	-
I	-	1	-	2	-		-	-	-	-	-	-
-	-		-	2	I	5	3	-			I	I
-	-	-	-	I	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	1	-	-
-	-	-	-	-	I	4	-	-	-	14	-	-
-	-	-	-	-	-	-	-	-	-	8	-	-
- 1	1	1	1	1	1	- 1	-	1	5	3	2	-
-	-	-	-	1	-	2	-	2	3	2	1	2
-	-	16	1	3	6	21	5	10	16	13	4	
-	-	-	-	-	-	1	-	-	-	2	1	1
-	-	3	-	-	-	-	-	-	-	-	-	-
-	-	2	1	2	3	6	2	3	31	9	6	3
-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	1	-	-	-	-	-	-	-
27	35	2	-	1	1	2	-	-	2	3	1	1
-	-	-	-	-	1	-	-	-	1	-	-	1
-	-	7	1	3	-	4	-	1	6	13	-	-
-	-	9	13	30	5	8	19	3	17	45	37	6
1	2	1	1	-	-	-	-	2	21	1	1	2
-	-	1	2	1	-	-	3	-	6	2	1	1
-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	2	-	-	-
-	-	-	-	-	-	-	-	-	1	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-
54	67	84	45	105	42	91	60	80	239	203	104	80

Appendix 1. (Cont.)

	Windblows Hav me						adows		
	C12	C13	M1	M2	M3	M4	M5		
Shannon index H.	1.011	1.025	0.985	1.117	0.979	0.802	0.659		
Eveness E.	0.840	0.753	0.723	0.799	0.709	0.682	0.611		
Pyrgus malvae (L., 1758)	-	-	-	1	1	-	-		
Carterocephalus palaemon (Pall., 1771)	4	6	-	4	5	4	_		
Thymelicus lineola (O 1808)	-	-	-	-	-	-	-		
Thymelicus sylvestris (Poda 1771)	2	4	1	7	3	-	-		
Ochlodes sylvanus (Esp. [1778])	3	19	8	17	4	3	3		
Papilio machaon L 1758	-	-	1	-	1	-	1		
Leptidea sinapis (l. 1758)/reali Reissinger 1989	9 1	3	3	6	6	2	-		
Anthocharis cardamines (I 1758)	<u> </u>	1	2	7	9	4	-		
Pieris brassicae (l. 1758)	-		2	-	1	2	4		
Pieris ranae (l. 1758)		5	<u>2</u> <u>1</u>	2	15	-	7		
Pieris nani (l. 1758)	Λ	3/	45	/8	89	12/	53		
$\frac{1}{Colias} \frac{1}{1} \frac{1}{1}$	-	-	-		1	-			
Conenterux rhamni (L. 1758)		20	16	1/	1	- 12	- 1		
$\frac{1}{1}$		20	- 10	14	-	-			
Collophric rubi (L. 1761)	-	-	-	- 1	-	-	-		
Cunido minimus (Euosslu, 1775)	-	-	-	-	-	-	-		
Capito minimus (Fuessiy, 1775)	-	- 7	-	-	- 7	-	-		
Celastinia argiolus (L., 1756)	-	Z	1	-	2	-	-		
Ancia agestis ([Defi. & Schift.], 1775)	-	-	-	-	-	-	-		
Polyommatus Icarus (Rott., 1775)	1	2	-	2	1	-	-		
Argynnis papnia (L., 1758)	-	2	2	-	-	6	4		
Argynnis adippe ([Den. & Schiff.], 1775)	-	8	1	2	1	1	-		
Issoria lathonia (L., 1758)	-	-	-	-	1	-	-		
Brenthis ino (Rott., 1775)	-	-	2	-	-	-	-		
Boloria euphrosyne (L., 1758)	-	-	-	-	-	-	-		
Boloria selene ([Den. & Schiff.], 1775)	10	62	-	3	-	-	-		
Boloría día (L., 1758)	-	3	-	-	-	-	-		
Vanessa atalanta (L., 1758)	1	1	1	-	7	-	1		
Vanessa cardui (L., 1758)	1	3	2	1	-	-	-		
Inachis io (L., 1758)	4	40	30	17	13	28	-		
Aglais urticae (L., 1758)	-	1	-	-	1	-	-		
Polygonia c-album (L., 1758)	-	-	4	1	5	7	1		
Araschnia levana (L., 1758)	12	3	5	37	25	5	3		
<i>Melitaea athalia</i> (Rott., 1775)	-	-	-	-	-	-	-		
Limenitis camilla (L., 1764)	-	-	-	-	-	-	-		
Apatura ilia ([Den. & Schiff.], 1775)	-	-	-	-	-	-	-		
Apatura iris (L., 1758)	-	-	-	-	-	-	-		
Pararge aegeria (L., 1758)	-	-	10	2	-	7	1		
Coenonympha arcania (L., 1761)	-	-	-	-	-	-	-		
Coenonympha pamphilus (L., 1758)	-	-	-	6	1	-	-		
Aphantopus hyperantus (L., 1758)	14	50	1	29	35	45	-		
Maniola jurtina (L., 1758)	1	3	45	21	30	21	37		
Melanargia galathea (L., 1758)	-	-	1	-	-	-	-		
Zygaena purpuralis (Brünn., 1763)	-	-	-	3	-	-	-		
/minos ([Den. & Schiff.], 1775)									
Zygaena viciae ([Den. & Schiff.], 1775)	-	1	1	4	-	-	-		
Zygaena filipendulae (L., 1758)	-	-	-	-	-	-	-		
Zygaena trifolii (Esp., 1783)	-	-	-	1	-	-	-		
Total	63	276	188	237	258	272	116		

Mu	Iched n	neadow	/S	Other meadows					Quarries and sandpits				
M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	Q1	Q2	Q3	S1
0.928	0.711	0.864	0.828	0.964	0.954	1.083	0.799	0.943	1.034	0.973	1.150	1.145	1.208
0.739	0.787	0.654	0.673	0.754	0.760	0.795	0.741	0.751	0.841	0.827	0.857	0.853	0.900
-	-	4	2	-	1	1	-	3	-	-	-	-	9
1	1	2	7	2	2	3	-	4	9	-	3	-	5
-	-	1	-	-	-	-	-	-	1	-	-	-	-
-	-	34	-	4	2	-	1	13	-	5	14	23	2
19	2	13	8	15	3	10	6	19	12	8	11	20	11
1	-	5	-	-	1	1	1	-	-	-	-	1	-
2	2	-	3	3	1	8	-	2	4	5	5	10	4
5	-	-	7	10	1	9	-	-	-	2	3	2	3
-	-	1	-	1	-	2	-	-	-	-	1	-	2
-	-	1	-	2	22	21	-	2	-	1	5	9	3
33	2	1	26	55	20	68	52	14	24	11	14	20	9
-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	-	6	3	3	3	7	18	15	7	5	3	5	13
1	-	-	-	-	2	-	-	-	-	-	2	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	1
-	-	-	-	-	-	-	-	-	-	-	26	7	-
-	-	-	-	1	-	-	-	-	2	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-
_	-	-	1	-	8	-	-	-	1	6	2	7	3
4	-	-	2	1	-	8	-	4	-	2	1	2	-
2	-	1	-	5	-	4	6	2	5	1	-	2	3
-	-	1	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	1	-	-	-	-
1	-	-	-	-	1	-	-	-	2	-	-	-	-
-	-	1	-	-	-	-	-	-	-	-	-	-	1
-	-	-	1	3	-	3	-	1	1	-	-	2	1
1	-	1	-	1	-	4	1	1	-	8	-	-	1
25	-	4	2	15	1	27	15	50	5	40	-	11	10
-	-	4	-	-	-	1	-	-	-	5	-	-	-
1	-	-	3	2	-	4	-	-	-	-	1	3	-
27	1	-	9	13	6	23	4	7	8	-	5	6	9
-	-	-	-	-	-	-	-	-	-	-	-	-	1
-	-	-	1	-	-	-	-	-	-	-	-	-	-
-	1	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	-	-	6	6	3	2	2	-	2	-	5	1	2
-	-	-	-	-	-	-	-	-	1	-	2	-	-
-	1	7	-	-	7	7	-	-	-	-	-	-	7
63	10	80	73	39	35	35	30	68	15	5	13	37	13
3	-	37	1	-	-	46	4	7	-	8	20	18	-
-	-	-	-	-	-	1	-	7	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	1	-
-	-	1	-	-	-	-	-	1	-	-	3	4	-
-	-	1	-	-	-	-	-	-	-	-	3	3	-
-	-	-	-	-	-	-	-	-	-	-	1	-	-
209	20	206	155	181	119	295	140	220	100	112	143	194	113

Apéndice 2. Descripción de las 38 parcelas del área de estudio "Oettinger Forst" (Baviera, Alemania).

N Size (ha) Habitat description

F1	> 10	Coniferous forest of <i>Picea abies</i> trees mostly older than 50 years, few grassy patches with very few flowering plants
F2	> 10	Humid mixed forest mostly composed of <i>Picea abies</i> trees of all age classes but also some <i>Fagus, Betula</i> and <i>Alnus</i> trees; several small ponds and sunny patches, <i>Molinia caerulea</i> abundant
F3	> 10	Humid mixed forest mostly with <i>Pinus sylvestris</i> trees (> 50 years), some <i>Betula</i> trees of different ages; many sunny areas and abundant grassy patches often dominated by <i>Molinia caerulea</i>
F4	1–2	Humid deciduous forest composed of alder, beech and oak trees, more than 50, often more than 100 years old; some grassy patches and few flowering plants
F5	> 10	Deciduous forest composed of beech and oak trees, some few spruce trees, trees more than 50, often more than 100 years old; some sunny grassy patches with flowering plants and some blackberry shrubs; <i>Lonicera</i> and <i>Lilium martagon</i> common
F6	> 10	Beech forest with trees of 80 years and more; only few grassy patches and rather few flowering plants
C1	2–5	Small windblows in a humid mixed forest (F2) often with <i>Agrostis stololifera</i> and <i>Digitalis purpurea</i> , at wet patches <i>Molinia caerulea</i> ; some of the clearings in rather early succession, but the majority with buckthorn bushes
C2	5–10	Windblow in early successional stage with <i>Digitalis purpurea</i> and <i>Atropa bella-donna</i> quite common; within the forest
C3	1–2	Wet windblow with many deep puddles, in early successional stage, <i>Digitalis purpurea</i> common, some <i>Cirsium palustre</i> ; flanking a little lake; within the forest
C4	> 10	Windblow in early successional stage, <i>Digitalis purpurea</i> common; flanking a little lake; within the forest
C5	> 10	Windblow in early successional stage, <i>Digitalis purpurea</i> common, some blackberry shrubs especially along forest roads; flanking a little lake and a small water course; within the forest
C6	1–2	Windblow in early successional stage, <i>Digitalis purpurea</i> and <i>Calamagrostis epigejos</i> common; within the forest
C7	> 10	Windblow in early successional stage, some deep puddles and humid area, larger areas with bare ground, <i>Digitalis purpurea</i> common; at the forest edge
C8	> 10	Windblow in early successional stage, <i>Digitalis purpurea</i> common, some flower rich patches along a forest road with blackberry shrubs, some humid areas; at the forest edge
С9	> 10	Windblow in early successional stage, very diverse vegetation structure from patches with bare ground to high growing meadow like structures, on a warm southern slope; at the forest edge
C10	2–5	Windblow in medium successional stage with <i>Calamagrostis epigejos, Rubus fruticosus agg, Digitalis purpurea</i> and some <i>Betula</i> shrubs; within the forest
C11	1–2	Windblow in medium successional stage with abundantly growing little spruce trees, <i>Digitalis purpurea</i> and <i>Calamagrostis epigejos</i> common; within the forest
C12	5–10	Windblow in medium successional stage, many young spruce trees and blackberry shrubs, <i>Calamagrostis epigejos</i> abundant; within the forest
C13	2–5	Windblow in medium successional stage with abundant buckthorn bushes and large thistle field (mostly <i>Cirsium arvense</i>) on a warm southern slope; within the forest

Appendix 2. (Cont.)

N :	Size (na) Habitat description
M1	2–5	Fertilised hay meadow (mown once a year) with Arrhenatherum elatius as dominant grass and with a thistle field of <i>Cirsium arvense</i> which was mown only in late summer; small humid edge with <i>Filipendula ulmaria</i> ; within the forest
M2	2–5	Fertilised hay meadow (mown once a year) with a greater variety of grass and herb species, one part mostly with <i>Urtica dioica</i> and <i>Cirsium arvense</i> ; part with <i>Iris sibirica</i> not mown; within the forest
M3	> 10	Fertilised hay meadow, mostly mown once a year, partly twice, sectors mowed at different times; <i>Holcus lanatus</i> as dominant grass; at the forest edge
M4	2–5	Fertilised hay meadow (mown once a year); <i>Arrhenatherum elatius</i> as dominant grass; one small edge with several <i>Cirsium</i> species remained not mown; at the forest edge
M5	> 10	Fertilised hay meadow (mown twice a year), <i>Arrhenatherum elatius</i> dominant; at the forest edge
M6	1–2	Mulched meadow, rather eutrophic so that <i>Urtica dioica</i> was partly dominant, some flowering plants at the edges (e.g. <i>Cirsium palustre</i>); within the forest
M7	< 1	Mulched meadow, mostly grassy vegetation (e.g. <i>Calamagrostis epigejos, Agrostis stololifera</i>); within the forest
M8	~1	Mulched meadow, partly fresh (e.g. <i>Cirsium arvense</i> common), partly humid (e.g. <i>Scirpus sylvaticus</i> common); at the forest edge
M9	1–2	Mulched and partly unmown meadow, the latter with many plants of <i>Urtica dioica</i> and generally high growing vegetation; within the forest
M10	1–2	Complex of fresh mulched and unmown humid meadow (the latter rather high growing with <i>Cirsium palustre, Urtica dioica, Phalaris arundinacea</i>) as well as a small field for game animals (cultivation of <i>Sinapis</i>); within the forest
M11	1–2	Partly mown (once a year) fresh and partly not mown humid meadow (<i>Equisetum</i> sylvaticum, Phalaris arundinacea, Scirpus sylvaticus, Iris pseudacorus and Lysimachia thyrsiflora common) and a small field for game animals (cultivation of Sinapis); within the forest
M12	2–5	Hay meadow (mown once a year) with small field for game animals; within the forest
M13	1–2	Unfertilised hay meadow (mown once a year) with mostly barren vegetation and a small field for game animals; a little water course within the patch, joined by <i>Cirsium palustre</i> ; within the forest
M14	2–5	Fallow meadow in medium successional stage with blackberry shrubs and some young spruce trees, <i>Calamagrostis epigejos</i> common; one larger thistle field (mainly <i>Cirsium arvense</i>); within the forest
M15	< 1	Not mown humid, high growing meadow; <i>Phalaris arundinacea</i> , <i>Scirpus sylvaticus</i> and <i>Iris pseudacorus</i> common; within the forest
Q1	2–5	Recent quarry with spontaneous vegetation (especially <i>Cirsium arvense</i>) and a lot of bare ground; within the forest
Q2	< 1	Old quarry with barren flower-rich grassland; <i>Anthyllis vulneraria</i> was quite common in the grassland, some initial <i>Betula</i> shrubs; within the forest
Q3	< 1	Old quarry with barren flower-rich grassland (comparable to Q2 but smaller and less barren), a thistle field (mainly <i>Cirsium arvense</i>) and <i>Betula</i> shrubs; within the forest
S1	~ 1	Old sandpit in medium successional stage but still large areas of uncovered ground, some rather humid areas and a pond, at some patches <i>Cirsium arvense, C. vulgare, Digitalis purpurea</i> and <i>Cytisus scoparius</i> abundant, some blackberry shrubs; within the forest