Changes in rank abundance of Microlepidoptera in The Netherlands

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Abstract: We investigated whether the pattern of abundance of 895 species of Microlepidoptera in The Netherlands has changed since 1850, and if such a change could be brought into relation with rarity, phenology and climatic effects. As a measure of abundance we took the number of records in the Tinea database since 1850, in ten progressively shorter periods. The species' abundances differed between the periods. We ranked the abundance of the species in each period separately, and calculated their change in rank (maximal - minimal observed rank). The median change was 441; in general common species (with highest average rank) have least changed rank, species of intermediate rarity the most. A positive correlation was found between a species' commonness and the slope of the regression of its rank values on the time, suggesting that over the whole study period rare species are receding relatively to the common ones. The pattern of change of rank abundance differs both among the spring-, early summer-, late summer- and autumn-flying species, and among the main families. Although we must caution that the randomness of the collection data in the database is limited, especially for the older material, we tentatively predict that a sample of moths taken today will contain less rare species than an equally sized sample in the past. Moreover, the composition of the fauna is strongly dynamic, implying that monitoring a few endangered species provides only incomplete information about the condition of nature.

Keywords: climate; cryptobiota conservation; dominance pattern; dynamics of abundance; phenology.

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Introduction

The species that compose a regional flora or fauna show widely different abundances. Some species are represented by only a few specimens, others occur in large numbers (Krebs, 1989; Williams, 1964). Terms like common and rare, applied in this context, either have an absolute or a relative meaning (Gaston, 1994).When exact numbers are available, such as the number of individuals, records, or census quadrates, at some arbitrary cut-off level the least numerous species are called rare in absolute terms, and the most numerous, common. In the present paper, however, we will consider rarity as a relative phenomenon (species are more or less rare, or common), and we will try to find out if a species' relative rarity is an invariant character, or rather an aspect that changes over longer periods of time.

There is a growing body of evidence that rarity of a species is connected with its biological characteristics (Byers & Meagher, 1997; Gaston, 1994; Gaston & Kunin, 1997; Gaston & Lawton, 1988; Inkinen, 1994; Orians, 1997). Nevertheless, the basic question whether or not species maintain a stable level of rarity over a time scale of decades, superimposed on the short-time fluctuations of population dynamics, is not quite resolved (Gaston, 1994; McGeoch & Chown, 1997; Williamson, 1987). There is a conviction among conservationists that common species are becoming commoner these days, and rare species rarer (Veling et al., 1997); although this is not stated explicitly, it is clear that rare and common are meant here in absolute terms. This conviction is far from easily tested, if only because the distribution of abundance over the species in a fauna, the dominance pattern, is not linear (fig. 1). In the present paper, we will address the assumption that rare species become progressively rarer by reducing the absolute counts to their rank numbers; in other words, we will use the values of the data points on the x-axis rather than those on the y-axis in the figure. Taken literally, the assumption would imply that the rank of abundance of the species should remain the same over time, because a steeper distribution of the data points in figure 1 would have no effect on the distribution of species along the horizontal axis. When the assumption is interpreted a bit more loosely, one would expect changes in rank order, while the direction and magnitude of the changes should be dependent on the rarity of the species.

This analysis also enabled us to address the validity of another, even more basic assumption, viz. the stability of the fauna at large. Although it is rarely put formally, most conservationists seem to assume that the pattern of abundance of a regional fauna is stable, except where human induced disturbances interfere (but see Hengeveld, 1986, and Samways, 1996). In fact this stability hypothesis forms the theoretical foundation of the current species-based approach to nature conservation that is widely adhered to both in political circles and in conservation services.

Since we had found earlier that the phenology seems to be affected by climate change (Ellis et al., 1997a; see also Beirne, 1947), we also investigated if changes in rank abundance might differ between species with different phenologies.

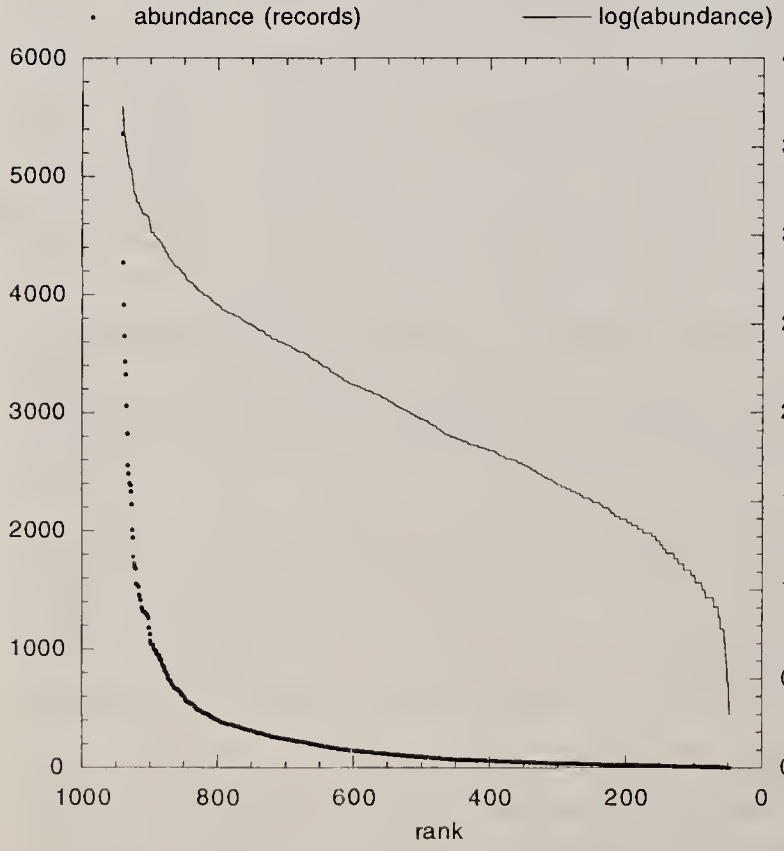

Fig. 1. Plot of species' abundance on species' rank over all 895 species used in the study (small dots, left axis). 'Abundance' is taken here as the total number of records in the time interval 1850-1997. Also the logarithm of the abundance is plotted (continuous line, right axis).

Material

The study is based on data about nearly 1400 species of Microlepidoptera found in The Netherlands stored in the Tinea database, which comprises approximately 370 000 records, covering a time span from about 1850 to the present day. All species recorded from The Netherlands are included in the study, except most families with leaf mining larvae (viz., Bedelliidae, Bucculatricidae, Coleophoridae, Eriocraniidae, Gracillariidae, Heliozelidae, Lyonetiidae, Nepticulidae and Tischeriidae). This limitation was needed because there is recently much activity to complete the faunistical pattern of the species of these families, which would give a spurious suggestion of a recent surge. Also, all species (and individuals) of which the identification was dubious were skipped, as well as all migrants, species that are storage or greenhouse pests, are regularly observed indoors, or are clearly aliens. To eliminate the effect of rare strays, also spe-

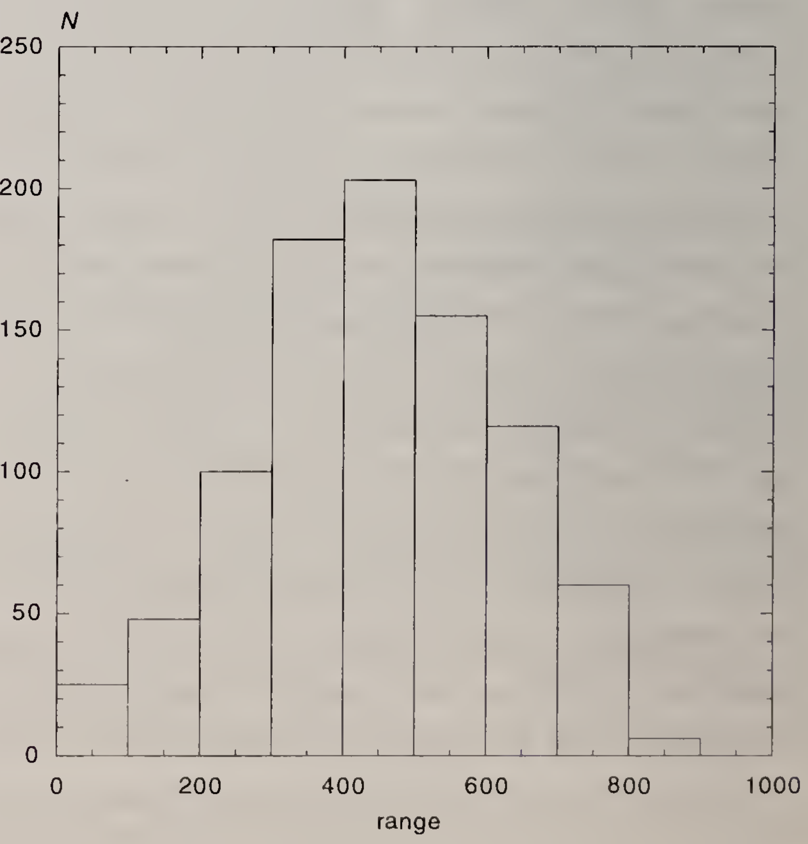

Fig. 2. Histogram of the range in ranks occupied by the species in the ten periods.

Table 1. The periods, their time ranges, their midpoints, the total number of records (*N*) summed over all species, and the total number of observed species (*S*).

period	from	to	incl.	midpoint	*N*	*S*
p850	1850	-	1899	1874.0	9752	698
p900	1900	-	1949	1924.0	11217	780
p950	1950	-	1959	1954.5	20274	543
p960	1960	-	1969	1964.5	22849	635
p970	1970	-	1974	1972.0	7129	651
p975	1975	-	1979	1977.0	14074	705
p980	1980	-	1984	1982.0	30597	792
p985	1985	-	1989	1986.0	43886	794
p990	1990	-	1994	1992.0	53361	799
p995	1995	-	1996	1995.5	17546	672

cies of which less than ten individuals were recorded were discarded from the study set that finally consisted of 895 species.

Methods

As a measure of abundance we used the number of records of a species in a given period (see Gaston, 1997, for a discussion of this and other parameters of abundance and rarity). We could not use the number of specimens collected, because the introduction of automatic light- and pheromone traps in the last decades raised the catch numbers appreciably. All developmental stages were taken into consideration.

We computed the species' level of abundance in ten periods (table 1). The periods differ in length, in order to have sufficiently high numbers to work on in each of them. Ranking of the abundance was done in ascending order, all families combined (note that this ranking differs from the customary 'top-ten' style of ranking). Ties, resulting from several species occupying the same number of records, were resolved by averaging the upper and lower bound of the ranks of the tied values. This procedure results in ten rank values per species. Because we are interested in a rising or declining trend for each species, the slope of the regression lines *b* of the rank on the time axis was calculated per species (midpoints of the periods were taken as x-values). To get an impression of the magnitude of the rank shifts of the species, the range of the rank values for each species were calculated as the difference of maximum rank and minimum rank of the species. The relative rarity or commonness of a species over the whole period 1850-1997 is expressed by the sum of its ten rank values, its 'rank sum'.

Some special attention was given to the periods p850 and p900, because they are both long in duration and antedate the global warming of our time. Moreover, the degradation of the quality of the natural landscape was not as strongly advanced until 1950. Therefore, it could be anticipated that there would be little difference in the dominance pattern during these two periods.

Phenological data were extracted from the database. Only records concerning adults that were collected in the field were taken into account. We calculated the running average of the number of records over an arbitrary period of 31 days, and selected the day with the highest values (or the mean, if there were more than two days) as the flight peak. The median flight peak, over all species, is on Julian calendar day 188 (July 7th). Specimens with flight peaks before day 151, within the range 151-187, 188-216, and after day 216 will be referred to as spring, early summer, late summer and autumn species, respectively.

We investigated if the four seasonal types differed in the median rank values in the ten periods (Friedman anova). We also calculated median values of the ranks per period for the seven main families, and tested if this value remained stable over time (Kruskal-Wallis anova).

To verify the stability of our results, we repeated our analysis, using as a measure of abundance the ranked number of 5x5 km squares in which a species was recorded. We also performed our calculations with z-transformed rank values (per species), and with an index based on the quotient of observed number of records per species and its expected value (expectations based on the marginal totals). Also, the same calculations were done on five, instead of ten periods. Trivial details apart, the results were identical to the ones reported below.

Results

The totals of records summed by period over all species are given in table 1. The *G*-distribution of the number of records over species and periods could not be calculated, due to numeric overflow, but the *P*-values of the individual rows was never over 0.00002 (based on the number of blocks, G_{adj}=11970.0195, df = 3222, $P < 0.0000$, pooling at 5). This demonstrates that species abundances have changed independently over time, and that the composition of the fauna is not invariant over time. Contrary to our expectation, there was a significant difference between p850 and p900 (G_{adj} = 3896.3385, df = 592; $P < 0.0000$).

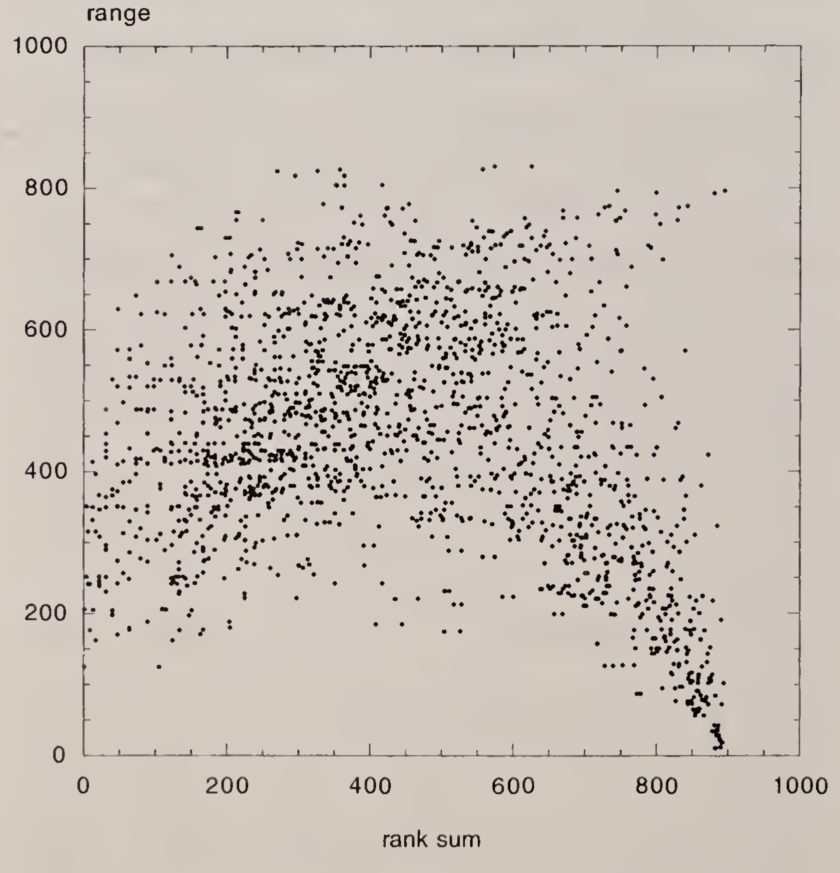

Fig. 3. Scatterplot of the relation between the range in ranks occupied by the species in the ten periods and the species' rank sum.

Figure 1 shows the distribution of the abundance, expressed as the total number records, for all species, sorted in descending order. Clearly, the distribution follows a lognormal distribution. Figure 2 gives a histogram of the range in rank for each species. It is clear that large changes in rank are the rule, rather than the exception: the median width of the range is no less than 441. The ranges are widest among the species with intermediate rarity (rank sum), while the most abundant species generally have the narrowest ranges (fig. 3).

Unlike the ranges, the values of linear regression of the ranks on the time axis for each species *(b)* are not normally distributed (fig. 4, Kolmogorov-Smirnov test, $P < 0.05$). The values of *b* are positively correlated with the species' rank sum (fig. 5; Spearman's R = 0.2768, N = 895, $P < 0.0000$). This means that the balance in abundance of the rare and common species is shifting towards to common ones. This was corroborated in two ways. First, species were divided in two almost equal groups according to the raw total number of records (N_1 = 446, sum ranging from 2 to 89; N_2 = 449, sum between 90 and 5632); then the total number of records in these two categories were calculated for the ten periods. The contribution of the group of rarer species to the periods' records sum shows a clear decline

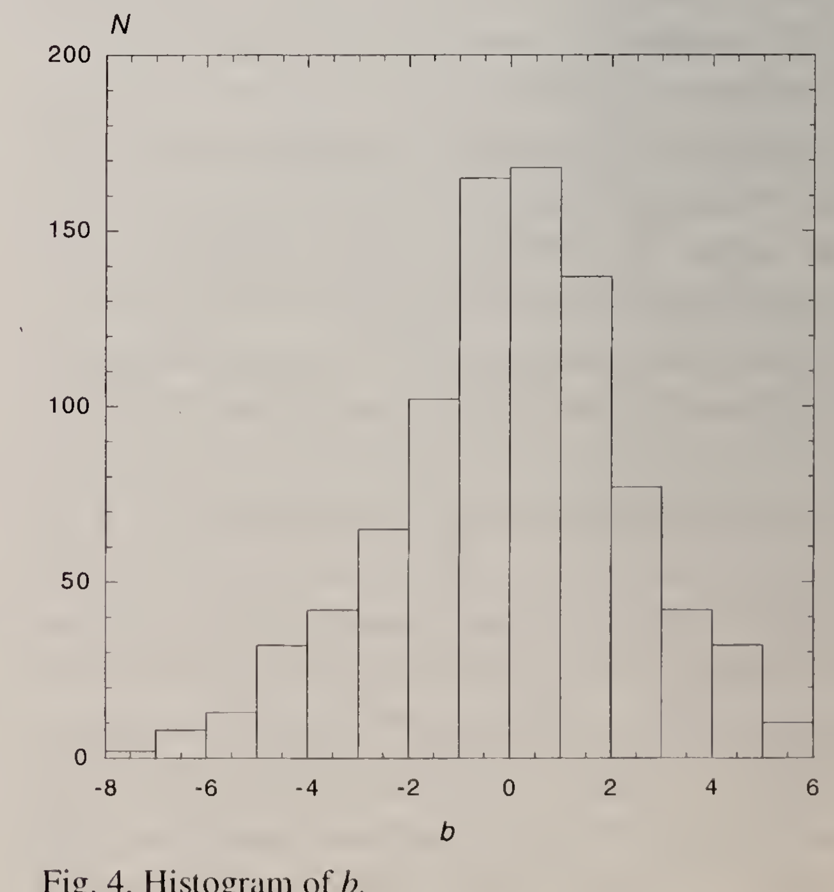

Fig. 4. Histogram of *b*.

Table 2. Species are split into two equal-sized groups according to the total number of records over all periods; columns 2-4 show the total number of records per period in both groups, and the percentage of the ''low'' group of the total. Columns 5-7 show the same, after dividing according to *b*. Finally, the evenness is shown.

	sum			*b*			
	low	high	% low	low	high	% low	evenness
p850	2635	7117	27.0	6970	2782	71.5	0.94
p900	1897	9320	16.9	6999	4218	62.4	0.89
p950	435	19839	2.1	6312	13962	31.1	0.71
p960	786	22063	3.4	10026	12823	43.9	0.78
p970	730	6399	10.2	3462	3667	48.6	0.88
p975	1107	12967	7.9	5408	8666	38.4	0.89
p980	2508	28089	8.2	10222	20375	33.4	0.89
p985	2852	41034	6.5	13739	30147	31.3	0.88
p990	3278	50083	6.1	16641	36720	31.2	0.87
p995	907	16639	5.2	5235	12311	29.8	0.87

(table 2). The same result was obtained when species were divided according to *b* (N_1 = 447, *b* between -7.464 and 0.117; N_2 = 448, *b* between 0.120 and 5.766). Also the evenness, a much-used index to evaluate the dominance pattern in an ecosystem (Pielou, 1975) declines, albeit less strongly.

The median rank values of the four seasonal types differ significantly, except for the autumn species (Friedman anova; N = 136, 313, 325, and 120, respectively; t^2 = 41.0540, 25.7105, 43,8914, and 15.0503, respectively; $P < 0.0000$, < 0.0023, <0.00000. and < 0.0896, respectively). Figure 6 shows the distribution of the average values. Note that the spring and early summer species almost generally have a lower rank than the late summer and autumn species. Also, there is a suggestion in the graphs of opposite trends for the two groups of species. As may be expected from inspection of these graphs, *b* differs among the species belonging to the four seasonal types (Kruskal-Wallis anova, df = 3, H = 17.5151, P = 0.0006); however, this significance vanishes when p850 is left out.

The median value of *b* differs significantly among the seven largest families (Kruskal-

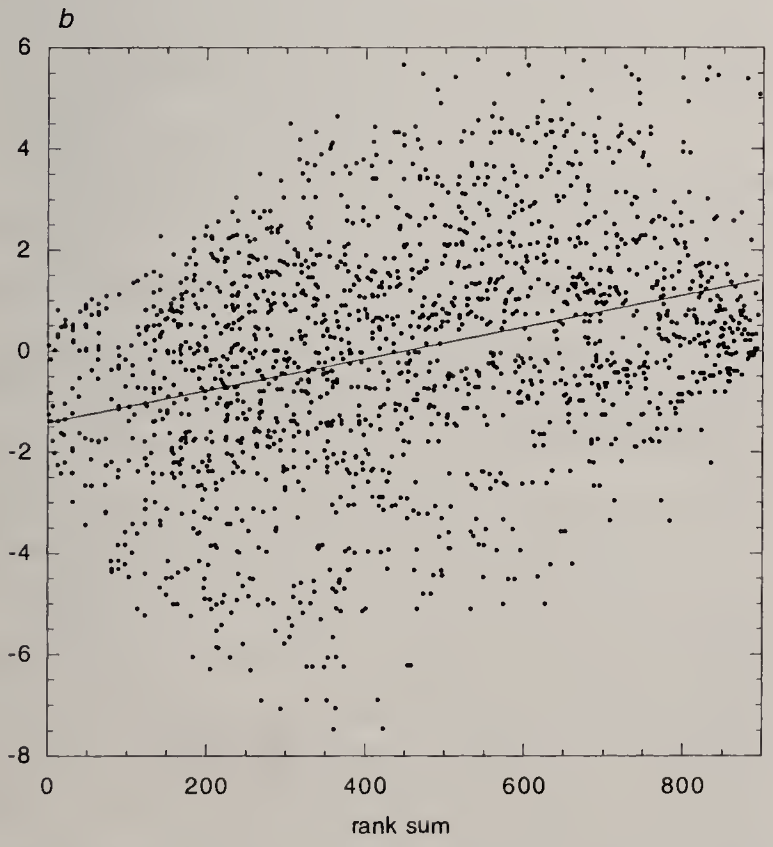

Fig. 5. Scatterplot of the relation of *b* with the species' rank sum. High-ranking (common) species have a significantly higher *b*, which indicates that they have become relatively even more common.

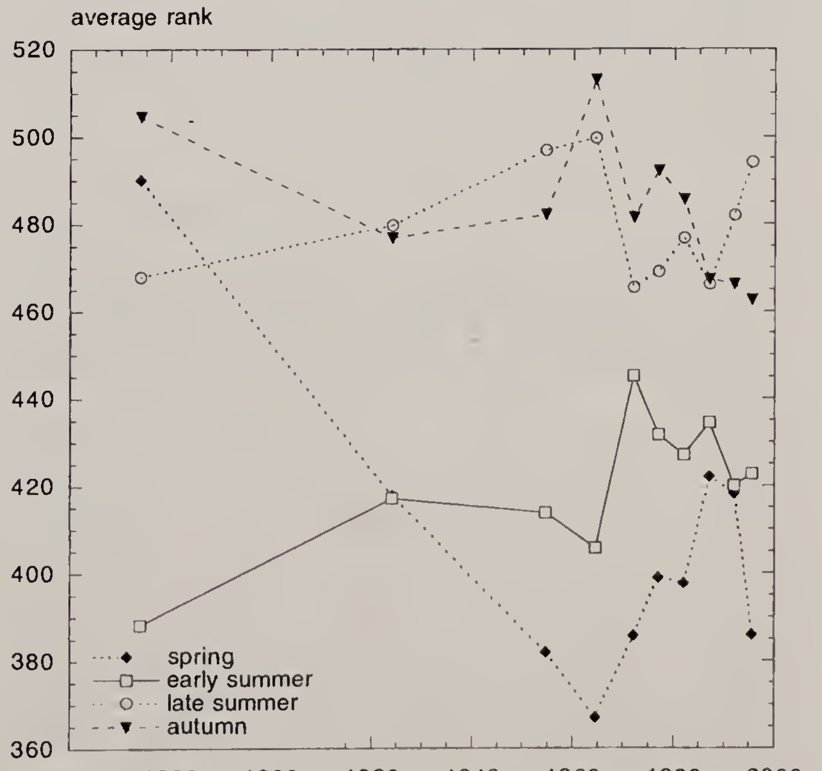

Fig. 6. Plot of the average rank values of the spring, early summer, late summer, and autumn species in the ten periods.

Wallis anova, df = 6, $N = 756$, $H = 42.9919$, $P = 0.0000$; median values are: Elachistidae -0.1431, Gelechiidae 0.7646, Oecophoridae -0.9611, Pterophoridae -0.9343, Pyralidae -0.4688, Tortricidae 0.5330 and Yponomeutidae 0.2781). In particular, the Oecophoridae and Pterophoridae are declining, while the opposite trend holds for the Gelechiidae and Tortricidae. This implies that innate biological traits that are correlated with taxonomic relationships, are responsible, at least partly, for the decline or expansion manifested by the individual species.

We finally calculated average rank values per period for the same seven families (fig. 7). Except for the Pterophoridae, all families showed strongly significant differences between the periods (Friedman anova; worst significance for the Elachistidae, $P < 0.0058$). The figure shows that families follow different trajectories, of which neither the optima nor the pessima clearly coincide.

Discussion

Our results indicate that the dominance pattern

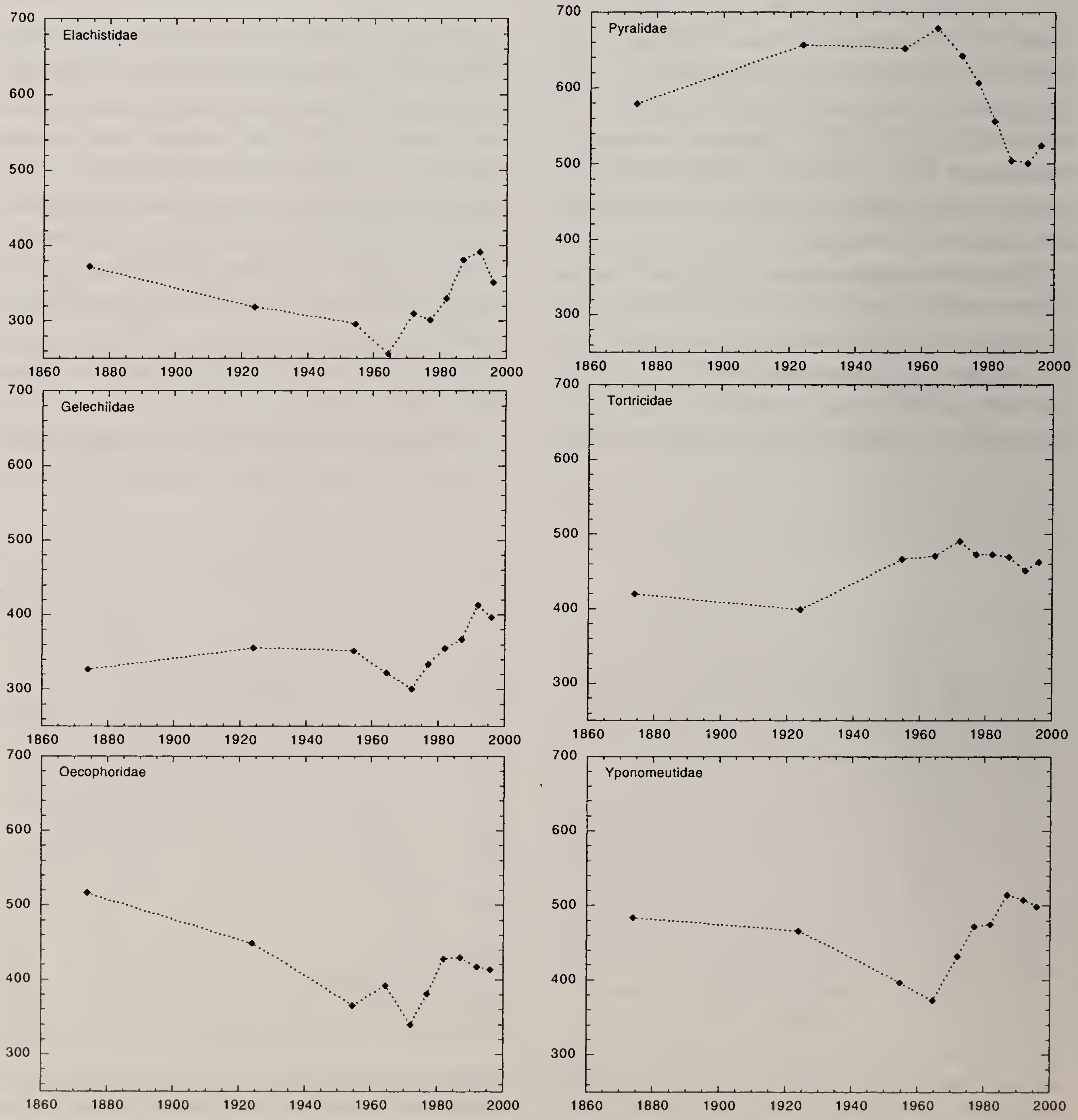

Fig. 7. Plot of the average rank values of the six main families.

of the species has changed strongly over time, and that both rarity and phenology are influential in this process. The direction of these relative changes do differ between common and rare species: species that, over the whole period, are the most numerous have shifted from lower to higher ranks, while the opposite holds in general for the least numerous species. Yet the erratic behaviour of the average values of ranks over time, should be a warning that it is unwise to make general statements over the full trajectory of 1850 to the present date. Taxonomic and phenological differences stand in the way of a general statement.

It is important to stipulate that our results are based on the assumption that the data in the database are randomly collected. This assumption at best is only approximately correct. Most records in the database of the pre-1950 period are based on material in collections, and the obvious limitations of space, the appeal of 'rarities' and disregard of the ordinary, and the limited number (and mobility) of collectors force us to regard our conclusions with great caution.

Moreover, as said already in the introduction, we cannot make statements about absolute changes in abundance. All that we can say is that, with the qualification just mentioned, we expect that a randomly collected batch of micros today will contain less rare species than a similar-sized collection in the past.

Comparable effects of relative rarity on the decline or expansion of species are recorded by Pollard et al. (1995) who found a range expansion for common British butterflies in the recent decades (1974 on). Also the results of Van Swaay (1990) seem to indicate that common species, contrary to rare species, have expanded their range in The Netherlands.

One would expect that largest changes in rank would mainly occur among the rarest species, because small changes in low record counts would entail large shifts in rank number. The fact that rather the species with intermediate abundance levels show strongest fluctuations in rank (fig. 3) therefore is somewhat surprising, and argues for the robustness of the methodology.

An inspection of the results down to the level of the individual species shows that most of the species with the highest or lowest value of *b* have already been recognised as such in a less quantitative fashion in the faunistical literature (cf. Kuchlein & Donner, 1993). The species that have declined most strongly are *Eurrhypis pollinalis* (Denis & Schiffermüller) and *Eudonia delunella* (Stainton); the two most in the lift are *Pammene fasciana* (Linnaeus) and *Diorycytra schuetzeella* Fuchs.

The rapid changes in average ranks, that follow courses that differ from one family to the other, are a striking result. If the progressive change of the landscape of The Netherlands were the main factor behind the changing pattern of rank abundances, a monotonous change would be the expected outcome. The pattern, or rather lack of it, that we found suggests that another main causative agent should be looked for. We believe this to be particular combinations of elements of the climate, be it (amount and/or distribution of) precipitation or any aspect of temperature, for which families may have their own specific requirements. We have little hope that it will be possible to isolate the precise combination of factors that is decisive in each family.

Also, the variation in average rank of the four seasonal types is suggestive of a climatic component. The global temperature rise is pronounced most strongly in winter temperatures (Shugart, 1998). Relatively warm winters may interfere with hibernation either through disruption of normal diapause, or by favouring moulds and other harmful organisms (Leather et al., 1993). It may also be that the shift to a later flight date, as we recorded before (Ellis et al., 1997a) could bring them in an less suitable light regime, or expose them to oviposition plants that have passed their favourable state (see also Graves & Reavey, 1996). Such a temporal mismatch would conceivably be most apparent in early spring. Also, as is vividly summarised by Schoonhoven et al., (1998), the nutritional value of foodplants changes appreciably in the course of the season, and warmer and drier summers could well have a negative effect, especially in autumn. It is interesting to note that p850 has intermediate average rank values when it comes to taxonomic distribution (fig. 7), but exceptional values for seasonal types, at least for early summer, and even more for spring species (fig. 6).

As to the hypothesis of faunal stability, we conclude that the dominance pattern of our entire Microlepidoptera fauna, rather than stable, is in a state of flux, like we have shown earlier for distribution of the Microlepidoptera fauna (Ellis et al., 1997b) or was shown for a local fauna by Kuchlein & Munsters (1988). The difference in the dominance patterns of p850 and p900, two periods that are outside of the time that the global rise in temperature became obvious (at least in comparison to what is happening nowadays) suggests that faunal dynamics are also strong in more or less undisturbed situations. Of course, there have been changes in land use in the course of these periods, but not to a scale and severity as has been witnessed since then. There remains a possibility that changes in methods of insect collecting, or in the balance of keeping and discarding specimens collected may be responsible for the changes observed; yet, the sheer dimension of the changes makes it improbable that these effects would seriously upset our conclusions.

We feel that is has been established that the Microlepidoptera fauna, and implicitly the cryptobiota at large, is like a running river, rather than a stable system. This means that is not advisable to concentrate on a restricted number of species for evaluation or long-term monitoring of the conservation status. In doing so, one may keep the salmon sharply in focus, but overlook that the river is changing all the time.

Samenvatting

Veranderingen en relatieve talrijkheid van Microlepidoptera in Nederland

We onderzochten of de verdeling van de talrijkheid van 895 soorten Microlepidoptera in Nederland sinds 1850 veranderd is, en of zo'n verandering in verband zou kunnen staan met zeldzaamheid, fenologie of klimaat. Als maat voor de talrijkheid gebruikten we het aantal records in de Tinea database sinds 1850 in tien steeds kortere perioden. De talrijkheid van de soorten verschilde tussen de perioden. We bepaalden voor alle soort het rangnummer van hun talrijkheid in elke periode en berekenden de mate van verandering van hun rangnummer (hoogste min laagste waargenomen rang). Deze veranderingen bleken zeer aanzienlijk te zijn: de mediane waarde bedroeg 441. In het algemeen verschoven de algemene soorten (met hoogste gemiddelde rangwaarden) het minst, en soorten van gemiddelde zeldzaamheid het meest. We vonden een positieve correlatie tussen de algemeenheid van een soort en de steilheid van de regressie van zijn rangwaarde op de tijd; dit suggereert dat sinds 1850 soorten met lage en gemiddelde rangwaarde in het algemeen in rang achteruit zijn gegaan ten opzichte van de soorten met hoge rang. Het patroon van verandering van de rangwaarden verschilt bij de soorten die vliegen in voorjaar, voorzomer, nazomer en herfst, en bij de grotere families. Hoewel we terughoudend moeten zijn omdat de gegevens in de database, zeker die voor de oudere collecties, geen aselecte steekproeven vormen, is onze voorzichtige conclusie dat een monster van micro's dat nú wordt genomen waarschijnlijk minder zeldzame soorten zal bevatten dan een monster uit het verleden. Bovendien is de samenstelling van de fauna zeer dynamisch, wat inhoudt dat het monitoren van een klein aantal zeldzame soorten slechts een onvolledig beeld geeft van de toestand van de natuur.

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