

Recent shifts in distribution of Microlepidoptera in The Netherlands

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Abstract: Possible changes in the pattern of distribution of Microlepidoptera species in The Netherlands in the last few decades were investigated. For that purpose the country was divided into six blocks, and the number of records of 104 species in the Tinea database before and after 1975 was counted. The results show that over 50% of the species have undergone a significant change in distribution. Changes are strongest in species for which the distribution limit crosses the country. Generally, the pattern of change shows a NW/SE opposition, matching the major trend in climatic isolines. Although these results cannot be interpreted as a testimony of a major recent climatic change, we assume that the pattern changes are climate-induced. Our results imply a strong dynamism in the composition of local biocenoses; moreover it demonstrates that, as far as the cryptobiota is concerned, there is little point in monitoring Red List species as parameters of the conservation status or value of protected areas.

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Introduction

In a previous paper (Ellis et al., 1997) we demonstrated that the flight peak of a large sample of Microlepidoptera in The Netherlands has shifted during the last twenty years to a date roughly eleven days earlier. In the same paper we suggested that this phenological shift, that is probably connected to the global change in temperature, might be accompanied by changes in the patterns of distribution. In the present paper the latter aspect will be analysed. Again we used the Tinea database as the source of our data.

Large, and mostly northward jumps of species are often recorded, but these usually are based on a few records, at the outer limit of the area of distribution. Examples for the fauna of The Netherlands include the sawfly *Corynis crassicornis* (Rossi) (Mol, 1988), the tortricid *Cydia amplana* (Hübner) (De Vos, 1991), the geometrid *Stegania trimaculata* (Villers) (Lempke & Ottenheim, 1989), and a number of Heteroptera (see Aukema, 1989). The more important, but often less spectacular “creep” of a species’ area by changes in abundance close to the area border are less frequently reported. Exceptions include the northward dis-

placement of the noctuid *Omphaloscelis lunosa* (Haworth) (De Vos & Zumkehr, 1995) and of *Thaumetopoea processionea* Linnaeus (Stigter & Romeijn, 1992), and the microlepidoptera *Phyllonorycter leucographella* Zeller (Stigter & Van Frankenhuyzen, 1991), *P. platanii* (Staudinger) (Kuchlein & Donner, 1993) and *Bucculatrix thoracella* (Thunberg) (Kuchlein & Van Frankenhuyzen, 1994).

An essential problem is that the information present in a database like that of Tinea has not been collected in a systematic way. This is a general problem with faunistic data, especially where it concerns the relatively poorly sampled cryptobiota. Moreover, negative data, i.e., the local absence of a species, are never recorded (if that can be established at all). Most importantly, the amount of information per region per year generally rises in the course of time, but not for all regions at the same pace. This prohibits a direct comparison of the distribution patterns in various periods. To put the question if there is a displacement of the fauna as a whole within The Netherlands therefore is like trying to pull oneself up by the hairs. But we can ask ourselves the more restricted question if the pattern of abundance of the species within The Netherlands has chan-

ged. We therefore will investigate if the relative (compared with all other species) abundance of each single species in parts of the country has changed over time.

Populations tend to be smallest and most widely scattered near the edge of the distributional area of a species. Ecological theory predicts that year-to-year fluctuations in population size will be largest in these peripheral populations (Brown, 1984; Hengeveld, 1990; Inkinen, 1994; Klomp, 1962; Lawton, 1995; Zeegers, 1991). Several species in our dataset have the border of their area of distribution crossing The Netherlands (table 1, data derived from table 10.8 in Kuchlein & Donner, 1993). We will test the prediction that these "peripheral" species have changed more than the "central" species, that live closer to their distribution centre.

Material and methods

We used a data set consisting of the records of 104 of the most common Microlepidoptera,

extracted from the Tinea database. All records concern adults, collected in the field. More details about the data set can be found in Ellis et al. (1997). All records were used this time; in particular there was no limitation as to the minimal number of records per species per year. We divided the country into six blocks: the same as the three sectors in the previous paper, with an additional east-west division (fig. 1). The number of records per species in the six blocks were counted, those from ≤ 1975 (a few dating back as far as 1850) separately from those ≥ 1976 . We have chosen 1975 as the pivotal year for two reasons: to have a sufficient number of old records to enable statistical treatment, and because there is a clear dip in the number of records around that year. As already remarked in the introduction, the number of records rises differently in the blocks (fig. 1). Records from before and after 1975 are referred to below as 'old' and 'new' records, respectively.

For each species we calculated an index which indicates the degree to which the spe-

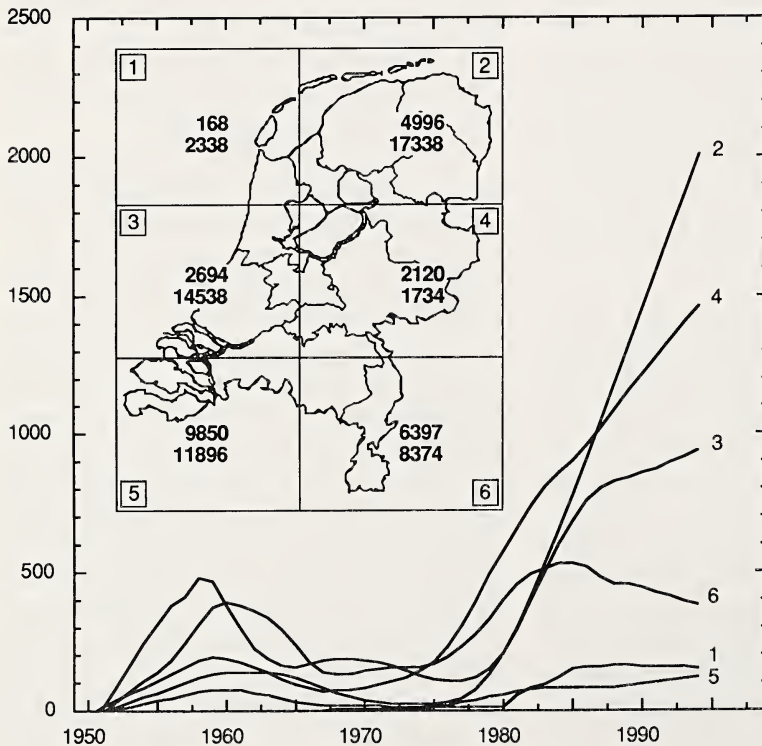


Fig. 1. Number of records per block per year. (Lines are smoothed curves, obtained by the locally weighted least square error method, taking 70% of the data into account; individual data-points not shown). The inset shows the arrangement of the blocks, and the total number of records per block before and after 1975.

cies has a "preference" for each of the blocks. The index (I), is based on the number of records observed in a block (X), divided by the number expected there (E) on the ground of the total number of records of the species and the general pattern of all species combined. E_{bs} is the number of records of a species s in block b if species s were distributed over the blocks like all species taken together; it is obtained by multiplying the total number of records of s by: the total number of records (over all species) in block b , divided by the total number of all records for all species and all blocks. I is calculated as a logarithm, because its value will be positive if X exceeds E (and their quotient is larger than 1), zero if X and E are equal, and negative if X is less than E . I was calculated for old and new records separately. The formulae are: $I_{bps} = \ln((X_{bsp} + 1)/E_{bsp})$. Here X_{bsp} = the number of records of species s in block b in period p ("old" or "new"), and $E_{bsp} = S_{sp} * B_{bp}/T_p$, where S_{sp} is total number of records of species s over all blocks in in period p , B_{bp} is the total number of records in block b in period p for all 104 species, and T_p is the total number of records of all 104 species over all blocks in period p .

The difference $D_{bs} = I_{bs,new} - I_{bs,old}$ then is an indication of the degree of change of preference of the species for block b . Because E is calculated for the periods and blocks separately, the effect of the unequal rise in observation density in the blocks is factored out. The value C_s , viz., the sum of the absolute value of D_{bs} over all blocks is a more global indication of the change in distribution pattern of the species.

To obtain an indication of the significance of the results, a small computer program was written that generated for each species separately a numerical approximation of the distribution of C . This was done by randomly assigning values to X_{bp} (with the constraint that $S_{s,new}$ and $S_{s,old}$ should remain the same) and calculating the ensuing C . 3000 repetitions were run per species, and the resulting distribution was compared with the observed values in a two-tailed test (using totals of 0.001, 0.01 and 0.05 percentiles). Because the values of X are free

to vary widely, and independently in the two periods, the test is quite severe; this was confirmed by some experiments with synthetic data sets.

Results

Table 1 gives for all species the values of $D_{b,new}$, and the significance of D_b and C . More than half of the species show a significant change in the pattern of their distribution. (Note that, for one species, the highest values of D are not necessarily the most strongly significant; this is because the width of distribution of the simulated values is strongly influenced by the value B_{bc}/B_{bm}). The values of D_{bs} are significantly positively correlated for blocks 1-2 (Spearman's $R = 0.340$, $P = 0.006$, Bonferroni correction applied) and blocks 1-3 ($R = 0.216$, $P = 0.041$). This suggests that the changes in distributional patterns very roughly show a NW-SE opposition.

The values of C_s for the peripheral species are significantly higher than for the central species; averages are 6.57 and 4.63, respectively (t -test; $df = 102$, $P = 0.008$).

Discussion

Our results show that over half of the species have undergone a significant shift of their regional pattern of abundance. A strong dynamism in the distribution of individual species in itself is not uncommon. A well-known example of a species with a fluctuating pattern of abundance in The Netherlands is *Araschnia levana* Linnaeus (Van Swaay, 1990; Tax, 1989); Pratt (1986-1987) documents similar expansions and contractions in *Polygonia c-album* Linnaeus in Great Britain. The result of our study is not so much that some species have shifted their distribution, but that so many have done so.

We assume that these shifts in distribution have a climatological background. This is indicated by the roughly NW/SE pattern that is found, because climatic isolines in the Netherlands in most cases show a SW/NE direction (cf. the KlimaAtlas van Nederland, 1972).

Table 1. List of the species used in the study, with: distribution (c: central species, p: peripheral species), the number of records before and after 1975, the values of D_b and C and the significance of D_b and C (*: $0.05 > P > 0.01$, **: $0.01 > P > 0.001$; ***: $0.001 > P$). Nomenclature follows Kuchlein & Donner (1993).

	c/p	N		D						C	significance						C
		≤'75	≥'76	1	2	3	4	5	6	D1	D2	D3	D4	D5	D6		
Adelidae																	
<i>Adela reaumurella</i>	c	69	569	-1.5	0.0	-0.8	-0.4	0.3	0.3	3.3	*	
<i>Nemophora degeerella</i>	c	54	471	-1.5	-0.4	0.2	-0.4	-0.2	-0.1	2.9	*	
Bucculatricidae																	
<i>Bucculatrix ulmella</i>	c	7	266	-4.3	-1.3	-0.8	0.9	-0.7	-0.9	8.9	.	.	***	.	.	.	
Choreutidae																	
<i>Anthophila fabriciana</i>	c	35	504	-1.5	0.3	-0.1	0.4	1.3	-0.7	4.3	
Coleophoridae																	
<i>Coleophora laricella</i>	p	6	141	-5.2	-1.4	0.0	-0.7	-1.3	-0.7	9.3	*	
<i>Coleophora serratella</i>	c	31	362	-2.8	-0.7	0.1	0.6	-0.8	-0.1	5.1	
Elachistidae																	
<i>Elachista apicipunctella</i>	c	10	86	-2.4	0.2	-0.6	-0.8	0.1	-0.1	4.2	.	*	.	.	.	*	
<i>Elachista cerusella</i>	c	82	497	-1.7	1.5	-0.5	0.8	0.3	0.7	5.4	.	*	
Gelechiidae																	
<i>Aristotelia dodicella</i>	c	8	144	-2.9	-1.8	0.0	-0.3	-2.1	0.3	7.4	.	.	.	*	.	.	
<i>Exoteleia dodecella</i>	c	12	180	-3.3	-1.0	-1.3	-0.2	0.5	-0.3	6.7	
<i>Neofaculta ericetella</i>	p	23	311	-0.8	-0.2	-0.6	-1.0	0.3	-0.2	3.1	*	
<i>Telediodes proximella</i>	c	19	269	-2.2	-0.7	-0.7	-0.5	-0.1	0.1	4.4	
<i>Telediodes vulgella</i>	c	3	119	-5.7	-3.2	-0.8	-0.1	-0.6	-0.8	11.2	*	.	***	.	.	.	
Gracillariidae																	
<i>Caloptilia alchimiella</i>	c	75	589	-1.5	0.1	-0.4	0.4	0.9	-0.3	3.7	
<i>Phyllonorycter harrisella</i>	c	10	306	-4.0	-2.0	-1.2	0.6	-0.5	0.1	8.5	.	.	.	*	.	.	
<i>Phyllonorycter quercifoliella</i>	c	12	341	-2.6	-1.3	-1.2	0.2	0.4	0.4	6.1	
Incurvariidae																	
<i>Incurvaria masculella</i>	c	43	260	-2.3	1.7	-1.2	-0.4	-0.9	0.5	7.1	.	**	
Nepticulidae																	
<i>Ectoedemia albifasciella</i>	c	5	115	-4.6	-2.4	-1.9	0.6	-0.6	-0.1	10.2	.	.	***	.	.	.	
Oecophoridae																	
<i>Batia lunaris</i>	c	13	175	-2.6	0.0	-0.3	-0.9	0.6	0.4	4.9	
<i>Batia unitella</i>	p	22	266	-4.5	0.5	0.5	-0.1	-1.2	-0.1	7.0	*	
<i>Carcina quercana</i>	c	165	737	-0.4	1.2	-0.2	1.4	-0.5	-0.7	4.3	
<i>Dentisia stipella</i>	p	19	74	-2.1	0.4	-1.0	-0.8	-1.3	1.3	7.0	.	.	.	*	.	.	
<i>Diurnea jagella</i>	c	86	545	-1.8	0.9	-1.5	0.1	1.0	-0.1	5.5	
<i>Diurnea phryganella</i>	p	15	73	-3.5	0.2	0.1	-0.7	-0.7	0.2	5.5	
<i>Ethmia funerella</i>	p	30	225	-4.0	-3.0	-0.2	-0.1	1.5	-0.5	9.3	
<i>Pleurota bicostella</i>	c	25	84	-3.4	-0.9	-1.7	-0.9	0.1	1.1	8.1	
<i>Stathmopoda pedella</i>	c	9	148	-3.4	0.9	-1.9	-0.3	-0.9	-0.9	8.1	.	***	
Plutellidae																	
<i>Plutella xylostella</i>	c	484	1614	1.5	0.3	-0.2	0.2	0.3	-0.2	2.7	**	*	
Pterophoridae																	
<i>Platyptilia gonodactyla</i>	c	67	107	-2.6	-0.7	0.3	-0.4	1.4	0.4	5.8	
<i>Pterophorus pentadactyla</i>	c	79	303	-2.2	0.0	0.2	-1.1	1.1	0.2	4.9	
Pyralidae																	
<i>Agriphila inquatella</i>	c	408	410	1.4	1.7	0.0	-0.8	0.6	-0.6	5.2	*	
<i>Agriphila stramineella</i>	c	1240	1205	-0.4	0.5	-0.1	0.2	0.4	-0.1	1.7	**	
<i>Agriphila tristella</i>	c	1023	1307	-0.6	-0.1	0.2	-0.2	-0.1	-0.2	1.3	***	
<i>Anerastia lotiella</i>	c	223	276	0.2	1.5	0.0	-0.1	1.6	-0.1	3.5	
<i>Aphomia sociella</i>	c	375	471	-2.2	0.1	0.3	0.2	0.3	-0.4	3.6	*	
<i>Cataclysta lennata</i>	c	305	623	-1.7	0.5	0.1	-0.5	0.5	0.1	3.4	
<i>Catoptria margaritella</i>	c	267	261	-0.1	0.0	-1.0	-0.5	-0.3	0.3	2.1	**	
<i>Chilo phragmitella</i>	c	772	447	0.0	-0.2	0.3	-0.3	0.1	0.2	1.1	**	
<i>Chrysoteuchia culmella</i>	c	1167	1728	-0.7	0.2	0.1	0.2	0.2	-0.1	1.4	***	
<i>Crambus ericella</i>	c	158	111	-1.6	-1.3	-1.0	-0.5	1.2	0.9	6.5	
<i>Crambus lathoniellus</i>	c	772	1166	0.2	0.5	-0.5	-0.1	0.4	-0.3	2.1	**	
<i>Crambus pascuella</i>	c	521	417	1.5	0.1	-0.5	-0.1	0.2	0.4	2.9	**	
<i>Crambus perlella</i>	c	889	790	-0.4	0.8	0.2	0.3	0.3	0.0	1.9	***	
<i>Elophila nymphaeata</i>	c	458	413	-1.1	0.0	-0.3	-0.2	0.0	0.4	2.0	**	
<i>Endotracha flammecalis</i>	c	132	639	-1.5	0.7	0.6	-0.8	-0.9	0.3	4.8	
<i>Eurrhyncha hortulata</i>	c	603	1286	-1.8	0.1	-0.1	0.2	0.6	0.0	2.8	*	
<i>Evergestis forficalis</i>	c	543	741	-2.1	-0.2	0.0	0.4	0.0	-0.1	2.8	*	
<i>Hypsopygia costalis</i>	c	513	869	-0.8	0.5	0.1	0.1	0.4	-0.2	2.1	***	

Table 1. Continuation.

	c/p	N		D						C		significance					
		≤'75	≥'76	1	2	3	4	5	6	D1	D2	D3	D4	D5	D6	C	
<i>Metriostola betulae</i>	c	272	185	-0.7	0.1	-0.9	-0.1	1.7	0.5	4.0	
<i>Numonia adenella</i>	c	186	320	-1.5	0.4	0.3	0.3	-0.5	0.2	3.1	*	
<i>Ostrinia nubilalis</i>	c	266	312	-2.8	0.9	-0.2	0.2	1.2	0.3	5.7	
<i>Phycita roborella</i>	c	259	572	-0.7	0.1	0.4	-0.6	0.7	0.3	2.8	*	
<i>Pleuroptya ruralis</i>	c	648	889	-0.6	0.7	0.1	0.2	-0.3	-0.2	2.1	**	
<i>Pyrausta aurata</i>	c	286	552	-1.7	2.3	0.6	0.0	0.9	-1.0	6.6	.	*	
<i>Schoenobius forficella</i>	c	622	403	-0.5	-0.4	0.1	0.1	1.5	-0.7	3.2	*	
<i>Scoparia ambigualis</i>	c	389	1246	-0.3	-0.4	-0.4	-0.2	1.1	-0.1	2.5	**	
<i>Synapse punctalis</i>	c	238	473	-0.5	1.2	-0.4	-2.0	-0.1	-0.4	4.4	
Tischeriidae																	
<i>Tischeria ekebladella</i>	c	14	288	-3.2	-0.2	-0.2	-0.6	-1.4	1.0	6.5	
Tortricidae																	
<i>Agapeta hamana</i>	c	126	342	-1.4	0.4	0.4	-0.2	0.0	0.0	2.6	*	
<i>Aleimma loeflingiana</i>	c	82	402	-0.5	0.4	-0.6	-0.1	2.0	-0.1	3.7	
<i>Ancylis achatana</i>	c	20	317	-3.4	-0.4	0.7	-0.7	0.6	-0.4	6.1	
<i>Ancylis mitterbacheriana</i>	c	5	129	-4.6	-1.8	-0.4	-0.6	-0.9	-0.2	8.5	
<i>Apotomis betuletana</i>	c	219	375	0.2	0.0	-0.7	0.7	0.9	0.0	2.6	*	
<i>Archips podana</i>	c	2325	977	2.3	-0.7	1.0	-0.6	-0.9	0.4	5.8	**	
<i>Archips xylosteana</i>	c	505	534	-0.1	0.4	0.0	-0.2	0.4	-0.1	1.2	***	
<i>Bactra lancealana</i>	c	58	403	-1.0	1.6	-0.6	-0.5	0.6	0.3	4.5	.	*	
<i>Capua vulgana</i>	c	56	350	-1.8	-1.1	-0.3	-0.5	0.6	1.5	5.8	
<i>Celypha striana</i>	c	279	361	0.8	-1.2	-0.3	2.0	1.1	0.5	6.0	*	
<i>Choristoneura hebenstreitella</i>	c	46	150	-3.3	0.8	-0.2	-0.8	1.1	0.1	6.2	
<i>Clepsis consimilana</i>	c	45	446	-2.0	-0.7	0.6	-0.8	0.0	0.4	4.5	
<i>Clepsis spectrana</i>	c	1375	637	1.4	0.3	0.5	-0.4	-0.4	0.4	3.3	*	
<i>Cydia pomonella</i>	c	2353	444	1.4	-0.5	0.9	-0.4	0.0	0.1	3.3	*	
<i>Cydia splendana</i>	c	269	602	-0.3	0.2	0.0	0.6	0.0	-0.1	1.3	***	
<i>Epiblema cynosbatella</i>	c	51	213	-0.5	0.3	-0.3	0.5	1.1	-0.5	3.3	*	
<i>Epiblema rosaeocolana</i>	c	108	380	-0.2	-0.9	0.3	0.0	0.1	-0.2	1.7	**	
<i>Epiblema uddmanniana</i>	c	58	557	-0.9	-0.6	0.9	-0.3	-0.5	-0.3	3.5	
<i>Epinotia bilunana</i>	p	25	192	-3.4	0.0	0.5	-0.3	1.0	-0.7	5.8	
<i>Epinotia immundana</i>	c	32	451	-1.8	0.5	-0.7	-1.1	-0.1	-0.8	4.9	
<i>Epinotia nisella</i>	c	20	89	-1.2	0.1	-0.4	1.1	-1.0	-0.6	4.4	.	.	.	*	.	.	
<i>Epinotia solandriana</i>	c	41	180	-1.9	-0.5	-0.8	1.1	0.0	-0.5	4.8	
<i>Epinotia tedella</i>	c	14	165	-3.7	0.6	-1.2	-0.7	-0.2	-0.2	6.7	.	*	
<i>Epinotia tetraquetra</i>	c	12	140	-3.5	-2.1	-1.6	-0.4	0.4	1.7	9.9	*	.	
<i>Eucosma cana</i>	c	86	476	-0.6	1.9	-0.1	0.1	1.1	0.3	4.1	.	*	
<i>Eupoecilia angustana</i>	c	32	134	-1.2	-0.7	0.5	1.0	0.5	-0.9	4.8	
<i>Gypsonoma dealbana</i>	c	37	514	-2.1	-0.8	-0.4	0.7	1.3	0.3	5.7	
<i>Hedya dimidioalba</i>	c	412	678	0.9	0.1	0.0	0.7	0.9	-0.1	2.8	*	*	
<i>Lathronympha strigana</i>	p	38	249	-2.6	-0.3	0.4	-0.4	1.4	0.1	5.2	
<i>Olethreutes arcuella</i>	p	20	101	-1.8	0.1	-2.4	-0.9	1.2	0.6	7.0	.	.	*	.	.	.	
<i>Olethreutes bifasciana</i>	c	7	202	-1.4	-2.0	0.3	-0.9	0.4	-1.3	6.4	
<i>Olethreutes lacunana</i>	c	713	1898	0.7	-0.9	0.2	0.8	-0.5	0.6	3.6	*	
<i>Olethreutes schulziana</i>	c	25	308	-1.2	-0.6	-1.2	-1.6	-2.2	-2.7	9.6	*	*	
<i>Pandemis cerasana</i>	c	814	1128	1.6	-0.1	0.3	0.2	-0.8	-0.1	3.0	**	
<i>Rhopobota naevana</i>	c	37	409	-3.7	0.1	0.0	0.9	-0.7	-1.1	6.5	
<i>Tortricodes alternella</i>	c	55	420	-3.3	-0.3	-0.6	-0.1	1.5	-0.8	6.6	
<i>Tortrix viridana</i>	c	289	650	0.2	0.0	-0.6	0.7	2.7	0.3	4.6	
<i>Zeraphera isertana</i>	c	59	452	-1.9	-0.5	-0.2	1.5	0.2	-0.1	4.3	.	.	.	*	.	.	
Yponomeutidae																	
<i>Argyresthia bonnetella</i>	c	13	124	-2.4	-1.7	0.4	-0.5	1.0	-0.7	6.6	
<i>Argyresthia brockeella</i>	c	34	299	-2.0	-0.6	0.0	0.2	0.4	-1.0	4.2	
<i>Argyresthia conjugella</i>	c	31	423	-0.9	0.2	-1.4	-0.8	0.7	-0.6	4.5	
<i>Argyresthia goedartella</i>	c	70	802	-1.7	-0.3	0.5	0.1	-0.4	-1.4	4.4	
<i>Argyresthia pruniella</i>	c	34	220	-2.3	-0.5	0.3	0.4	0.1	-0.5	4.0	
<i>Argyresthia retinella</i>	c	21	323	-1.9	-0.1	0.3	0.2	0.0	-1.1	3.5	*	
<i>Yponomeuta evonymella</i>	c	191	763	-0.5	1.0	-0.4	1.3	2.0	0.1	5.3	
<i>Yponomeuta sedella</i>	p	16	154	-3.6	-0.7	-0.6	-0.5	-0.1	1.2	6.6	

This matches with the overall trend in distributional area limits recognised in The Netherlands by Kuchlein & Donner (1993). Another indication is found in the numerous reports in literature of strong recent northward range expansions, a few of which were referred to already in the Introduction. Our explanation is in agreement with the general opinion in literature on species distributions (e.g., Bruun, 1992; Dennis, 1993; Heath, 1975; Kaisila, 1962). A species' distribution is the result of its population dynamics (Sutherst et al., 1995), and this is determined to a large extent by climatic variables. Numerical simulations by Aspinall & Matthews (1994), working with *Carterocephalus palaemon* Pallas, and Williams & Liebhold (1995), who studied the forest defoliators *Choristoneura occidentalis* Freeman and *Lymantria dispar* (Linnaeus) indicate that relatively small changes in temperature and precipitation may result in strong distributional effects, that, moreover, are uncorrelated from one species to the other.

It must be borne in mind that we cannot decide upon our data whether the degree of distributional flux is "normal", or higher than in the last few centuries because of the ongoing global climatic change. Only a continued monitoring can make this clear. That a northward expansion has been going on already in the first half of the century is demonstrated by Kaisila (1962). Working on a huge amount of distributional data of Lepidoptera in Finland, Kaisila found two periods of strong expansion, one starting around 1910, the second around 1930, separated by a stationary or regressive period in between.

Locally, these area changes are translated in changes in the composition of the fauna. This is precisely what was found by Kuchlein & Munsters (1988) in the fauna of Stein (province of Limburg). In a comparison of the periods 1959-1963 and 1979-1985 it appeared that 17% of the species complement of Tortricidae + Pyralidae was lost in the second period, and 27% gained (32 and 59 species, respectively). Bruun (1992) daily operated a moth trap on the tiny island of Houtskär in the Baltic Sea for from 1954 up to 1989, with on-

ly two interruptions of a week each. He too found a dynamic fauna (10 species settled in this period, and 158 disappeared, although it must be acknowledged that part of that is attributed to toxic fallout after the Chernobyl disaster). More examples can be found in Udvardy (1969), who himself is a strong advocate of faunal dynamism.

The effect of this to and fro in local densities is what was called "labile species associations" by Lawton (1995). In other words, the species assemblage at one place is inherently unstable, and the components of the food web change over time. This fits with Thomas' (1995) conclusion that many cryptobionts are restricted to a narrow time slice in the succession of a vegetation, and for that reason tend to occupy a habitat patch only for a limited number of years.

When species come and go at a place, be it through normal or unusually strong climatic vicissitudes, then there is little point in monitoring single species for the sake of evaluating the long-term ecological health or conservation status of a habitat. In other words, it may be a bad policy to focus strongly on Red List taxa for monitoring purposes as a stand-in for the ecosystem as a whole. It has been argued that cryptobionts, with their generally short to very short generation time, in nature have an inherently chaotic pattern of population dynamism (Zeegers & Van Veen, 1989). This element of chaos, compounded with that of a response to climatic change, make cryptobiotic species generally inappropriate long-term monitor species. Moreover, as was corroborated by our results, populations change most strongly the more one approaches the distributional margin of a species. Thus, precisely in the part of its area where a species tends to be rarest, and has the highest change of obtaining Red List status, it is most difficult to sensibly monitor the species. Added to the other limitations of Red Data Lists for the cryptobiota (too many badly known groups, too few people capable to identify them, lists grow to unwieldy length) this argues for the selection of other parameters rather than number of Red List species, as a yardstick of conservation value or status of a site.

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