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Contrasting trends of butterfly species preferring semi-natural grasslands, field margins and forest edges in northern Europe

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Abstract Indicator classifications help us to focus on the most relevant groups of species in monitoring the effects of land use changes on biodiversity. We studied changes in distribution area of 74 butterfly species preferring one of the three common habitats of boreal agricultural landscapes: semi-natural grasslands (35 species), arable field margins (7) and forest edges (32). Using extensive atlas data from four time periods during the last 50 years in Finland, we quantified trends in the occupancy of the species in 10 km grid squares, and classified them into four classes: declining (23), stable (17), increasing (27) and fluctuating (7) species. Trends among the species favouring three habitats were different: 60% of the species of semi-natural grasslands had declined, whereas 86% of the species typical of open field margins had increased. An increase also predominated in species associated with forest edges. Declining and increasing species differed in three ecological characteristics: increasing species were more mobile, utilized a wider range of habitats and, based on their larval host plants, lived in more eutrophic habitats than declining species. Species overwintering as adults showed more positive trends in occupancy than species overwintering as eggs, larvae or pupae. Observed trends in occupancy are in good agreement with long-term changes in land use and habitat availability in Finland: a long-continued decrease in the area of semi-natural grasslands and an increased amount of open forest edges and clearings due to modern forestry during the past 50 years.

Keywords Agricultural landscape · Atlas data · Indicator classification · Change in distribution area · Species trait

Introduction

There is much need for useful indicators in monitoring the effects of land use changes on biodiversity. For example, several kinds of indicators at various spatial levels are needed for assessing whether the Convention of Biological Diversity's 2010 target (UNEP 2006)—a significant reduction in the current rate of biodiversity loss on global, regional and national levels—will be achieved (Balmford et al. 2005a, b). In order to cover various kinds of terrestrial, marine and freshwater habitats, indicators are needed from different taxonomic groups. A separate consideration of different taxonomic groups may also be necessary within terrestrial habitats, since there are major differences between taxonomic groups in their sensitivity to environmental change (Thomas et al. 2004).

In order to effectively monitor the consequences of specific land use changes for biodiversity, it is necessary to restrict the focus to the species associated with a particular habitat. For example, Gregory et al. (2005) found a difference between the population trends of European farmland and woodland birds. They attributed the decline, observed in farmland but not in woodland birds, to agricultural intensification. In less mobile organisms, such as plants and insects,

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associations with specific habitats may be stronger as individuals often spend their entire life within one habitat patch. Higher habitat specificity and shorter generation time are among the likely causes behind the observation of Thomas et al. (2004), demonstrating that butterflies had experienced steeper declines than birds in Britain. The first attempt towards developing a European level indicator of population trends in butterflies was recently made by van Swaay and van Strien (2005). It was based on data from transect monitoring schemes in nine European countries and followed the methodology developed earlier for birds by Gregory et al. (2005). The results showed almost a 50% decline in the abundance of grassland butterflies over a time period of 15 years.

Butterflies are a particularly useful indicator group in open habitats (Erhardt and Thomas 1991; Thomas 2005), and therefore they were selected as one of the taxa that are actively monitored in agricultural landscapes of Finland (Kuussaari et al. 2000). In this paper, we focus on changes in the distribution area of the butterfly species occurring in Finnish agricultural landscapes based on atlas data. Previous studies on distributional changes of butterflies based on grid square data on various spatial scales have indicated that studies of occupancy in 10 km squares generally underestimate declines and even fail to detect declines especially of common species (Thomas and Abery 1995; Cowley et al. 1999; León-Córtes et al. 1999, 2000). However, there are also several strengths in the use of atlas data: they tend to be available from larger numbers of replicate areas, for a larger number of species and from longer time periods than quantitative transect count data. Many previous reports on changes in distribution areas of butterflies in western Europe have been based on 10 km or 5 km atlas data (Heath et al. 1984; van Swaay 1990, 1995; Prendergast and Eversham 1995; Warren et al. 1997, 2001; Maes and van Dyck 2001; Thomas et al. 2004).

In this paper we quantify changes in the occupancy of 74 butterfly species in 10 km × 10 km squares in Finland during the last ca 50 years. Based on observed changes in occupancy, we classify the species into declining, stable, increasing and fluctuating species and analyse whether trends in occupancy differ between the butterfly species of different habitats. In addition to the association between species habitat preferences and trends in occupancy, we study whether the trends are associated with species traits, following the recent studies by Maes and van Dyck (2001), Kotiaho et al. (2005), Öckinger et al. (2006) and Wenzel et al. (2006). Specifically we analyse whether declining and increasing butterfly species differ in their average host specificity, habitat breadth, nutrient status of the breeding habitat and mobility, and whether average trends in occupancy differ between species groups varying in their overwintering stage and larval host plant growth form.

Material and methods

Butterfly atlas data

We used all available butterfly atlas data for the 74 focal butterfly species of agricultural landscapes (Pitkänen et al. 2001) gathered in Finland before the year 2004 (Huldén et al. 2000; Saarinen et al. 2003) and divided these data into four study periods with reasonably equal amounts of data within each study period: before 1960, 1960–1990, 1991–1998 and 1999–2003 (Table 1). In the analyses we focused on changes in the occupancy of species in 10 km × 10 km grid squares during the four time periods.

Records before 1991 were collected by the Finnish Museum of Natural History from various sources including a large number of butterfly collections of amateur lepidopterists and natural history museums as well as results of local surveys of butterfly occurrence.

Table 1 Summary of the atlas data used in the analyses of changes in distribution areas of butterflies during the four study periods

	Observation period			
	<1960	1960–1990	1991–1998	1999–2003
Median year of observation[a]	1955	1985	1995	2001
Number of records				
All data[b]	15,222	38,225	51,990	51,559
Squares with ≥40 records	9,753	29,778	44,568	43,161
Number of study squares				
with ≥1 records	727	1,244	1,044	1,053
with ≥10 records	294	552	626	682
with ≥40 records	90	251	346	349
with ≥100 records	33	92	153	157
Selected well-studied squares (n = 141)	90	97	95	100
Number of records	9,753	14,434	18,111	16,922
Percentage of all records for the period	64.1	37.8	34.8	32.8
Mean number of records/square	108.4	148.8	190.6	169.2

[a] In the cases of records from a longer period than 1 year, the last year of the recording period was used in the calculations of the median year of observation

[b] Excluding the records of the insect mapping project for 10 butterfly species during 1981–1996 (Hyönteiskartoitus/Insektkartering 81 1996) and the records of *Parnassius apollo* collected in an extensive single species mapping project (Mikkola 1979)

They were published in the Atlas of Finnish Macrolepidoptera by Huldén et al. (2000). The spatial and temporal precision of these records varies considerably. We excluded from our analyses all records without precise information on the 10 km observation square, as well as all records, which did not fit completely within any single one of our four study periods. In order to avoid biased results in the analyses of trends in occupancy, we also excluded the records of two special mapping schemes focusing only on a subset of species, which were included in the museum atlas database. These two data sets included the records of 10 butterfly species in an insect mapping project during 1981–1996 (totally 43,316 records; Hyönteiskartoitus/Insektkartering 81 1996) and the records of *Parnassius apollo* collected in an extensive single species-mapping project (totally 1,402 records; Mikkola 1979).

The records from the last two study periods (1991–1998 and 1999–2003) were collected in the National Butterfly Recording Scheme in Finland (NAFI; Saarinen et al. 2003). The precision of these records is generally better than in the older data, because in NAFI records are accepted only from a single year and a single 10 km square on one recording sheet. In NAFI the emphasis is on collecting monitoring data on the occurrence and abundances of all butterfly species present in a 10 km squares. All records of the database of NAFI were considered suitable for analysing trends in the occupancy of 10 km squares. The nomenclature of this paper follows Kullberg et al. (2002).

Quality of atlas data

Because of the qualitative differences in the butterfly records before and since 1991, there may also be differences in the species which have been comprehensively recorded during the four study periods. It is well known that rare species tend to be over-represented and common species under-represented in older museum and other natural history data when compared to more systematic field mapping projects (e.g. van Swaay 1990; McCarthy 1998). Although rare species may also be over-represented in more systematic surveys such as NAFI, it is likely that the NAFI records from the last 13 years better reflect the actual occurrence of common and rare species in Finland than the records of older atlas data.

In order to examine whether there are differences in the proportions of rare and common species between the datasets from the four study periods, we used information on the contemporary rarity of the species from four Finnish handbooks of butterflies. We classified the 74 focal species into six rarity classes separately for each of the four time periods: 1 = very rare, 2 = rare, 3 = moderately rare, 4 = moderately common, 5 = common and 6 = very common. For the records before 1960 we used a rarity classification based on Valle (1935) with help from Aro (1900) in the case of the few species for which the rarity class was not entirely clear based on the text of Valle. For the butterfly records from the periods 1960–1990 and 1991–1998 we used a rarity classification based on Marttila et al. (1992) and for the last study period 1999–2003 a classification based on Marttila et al. (2000).

In order to compare the distributions of records in the six rarity classes between the four study periods, the percentages of records within different rarity classes were calculated separately for each study period. For each species within each study period we first calculated the percentage of all the records for that time period. Using these values, we then calculated between-species mean percentages of records and their standard errors for each rarity class within each time period.

Study effort and trends in occupancy

Study effort fundamentally affects the results of distribution mapping programs (Dennis et al. 1999; Dennis and Thomas 2000). Variation in study effort may potentially mask existing population trends or produce spurious trends. Thus, we calculated trends in occupancy separately using four datasets with a varying minimum study effort required for a particular study square to be included in the analyses. The four data sets included the study squares with ≥ 1, ≥ 10, ≥ 40 or ≥ 100 total records within a study period. A record was defined as an observation of at least one individual of any species in the focal square during a study period. Occupancy of each butterfly species was then calculated for each study square based on the available records within the focal study period. The resulting temporal trends in occupancy of each species based on the four differently constrained data sets were then compared with each other to assist selection of adequate sample size for further analyses.

Selection of study squares

Based on the examination of the effect of study effort on observed trends in occupancy, we decided to focus only on the most comprehensively studied 10 km squares in the statistical analyses. We included all the squares with a minimum total of 40 records during the first time period ($n = 90$) in the analyses, and the same study squares during the three sub-

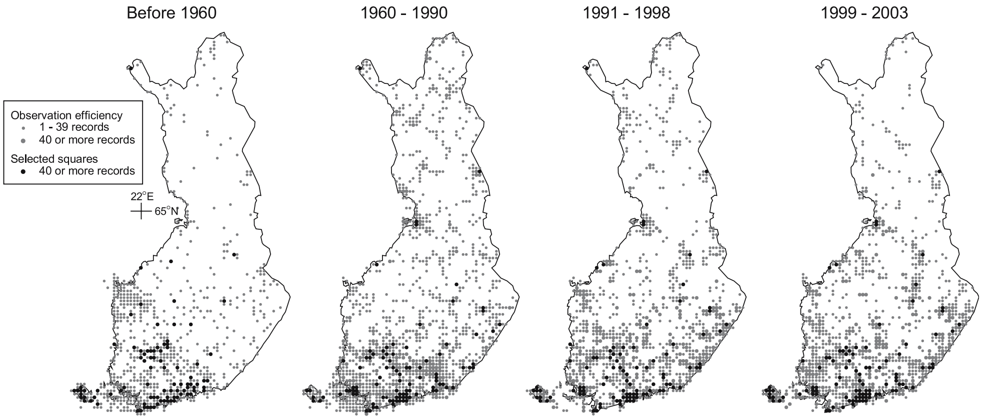

Fig. 1 Maps of the locations of the records of the studied 74 butterfly species for the four study periods. The well-studied 141 squares included in the analyses of trends during the four study periods are shown in black

sequent time periods in those cases when they had been equally well studied (resulting in a total of 229 replicates from the 90 squares). In addition, we included all the squares which were sufficiently well studied (≥40 records) in all the three last time periods (n = 51 squares) in order to equalize the number of studied squares for each time period to 90–100 replicates. This selection procedure resulted in a total of 141 study squares with a total of 382 replicates during the four time periods (Table 1; Fig. 1). The locations of the selected squares concentrated in the main agricultural areas of southern Finland, which is also the geographic area of highest butterfly species richness in Finland. The study squares included regions of both intensively and less intensively cultivated agricultural areas.

Analyses of trends in occupancy

For each species the trends in the occupancies of the selected 10 km squares during the four time periods were analysed using generalized linear mixed models with penalized quasi-likelihood (GLMM PQL). Study square was included in the models as a random variable (Venables and Ripley 2002). In addition to the examination of linear trends, the significance of the curvi-linear second and third order polynomials was tested in order to detect also non-linear and fluctuating trends in occupancy. GLMM analyses were conducted using the statistical package R version 2.0.1 (R Development Core Team 2004). The results of the GLMM as well as plots of the fitted GLM with their 95% confidence limits were used in the classification of species into the four trend categories. To solve borderline cases in the classification we checked the trends in a larger sample of well-surveyed squares from the last two study periods (210 squares with ≥40 records during both last study periods).

Trend in occupancy and habitat preference

We analysed the association between trend in occupancy and habitat preference of the species based on the habitat preference classification presented by Pitkänen et al. (2001). They defined 74 species typically occurring in agricultural landscapes in Finland by excluding species which were (1) confined to bogs and subarctic and arctic areas in Lapland, (2) rare migrants and (3) a few rare species currently confined to open esker areas with sandy soil or open rocky areas not close to agricultural areas. The rest of the species were classified according to their habitat preference into species of three common habitat types in boreal agricultural landscapes: open field margins and farmyards (7 species), semi-natural grasslands (35 species) and forest edges and clearings (32 species). In contrast to many agricultural areas of central and western Europe, open edges of forests and cultivated fields represent a common habitat type in boreal agricultural landscapes which are typically mosaics of cultivated fields and forests (Virkkala et al. 2004). For example in Finland 67% of the land area is covered by forest land and only 9% by agricultural land (Anonymous 2005). The species associated with forest edges are likely to be less affected by agricultural practices than the species of grasslands and field margins, because the species of forest edges can also occur in forest landscapes with no agricultural use at all. The habitat classification of species was based on Finnish butterfly handbooks and an expert evaluation. Recently, an NMDS ordination (McCune and Grace 2002) and an indicator species analysis (Dufréne and Legendre 1997) based on quantitative transect count data strongly supported this classification (M. Kuussaari and J. Heliölä, unpublished).

We tested whether average trends in occupancy differed between the species of the three habitats with the Kruskal–Wallis test followed by Tukey's pair-wise comparisons using the statistical package Statistix 8 (Analytical Software, Tallahassee, Florida, USA). In this analysis the occupancy trend classes were coded as follows: declining = –1, stable = 0 and increasing species = 1. Fluctuating species were omitted from this analysis.

Trends in occupancy and other species traits

We conducted two types of statistical analyses to examine whether trends in occupancy of the 74 species were associated with species traits other than habitat preference. When the species trait could be measured as a continuous or ranked variable (host specificity, habitat breadth, nutrient status of the breeding habitat and mobility; see Appendix), we used the Mann–Whitney *U*-test to study whether there was a difference in the average values of the traits between the declining ($n = 23$) and increasing ($n = 27$) butterfly species. When the species trait was measured as a categorical variable (overwintering stage and larval host plant growth form; Appendix), we used the Kruskal–Wallis test followed by Tukey's pair-wise comparisons to test whether average trends in occupancy differed between the categories of the species traits. Stable species were included in these analyses similarly as in the analysis comparing the trends of the species preferring the three habitat types. These analyses were conducted using the statistical package Statistix 8.

We measured larval host plant specificity, and habitat breadth and mobility of the adult butterflies using the values published by Komonen et al. (2004). They listed estimates of these variables for 67 of our 74 focal species. We used the same logic and literature as Komonen et al. in order to fill in missing values for the four common migratory (*Pieris brassicae*, *P. rapae*, *Vanessa atalanta*, *V. cardui*), two extinct (*Maniola lycaon*, *Lasiommata megera*) and one "irruptive" (*Lycaena dispar*) species in Finland not considered by Komonen and his colleagues. Host specificity was measured as a three-class variable: 1 = monophagous, 2 = oligophagous and 3 = polyphagous species. The missing values for the seven species were estimated based on Huldén et al. (2000). Habitat breadth was measured as a three-class variable indicating the number of habitat types occupied by the butterfly species: 1 = one, 2 = two and 3 = three or four relatively broad habitat types described by Komonen et al. (2004). The missing values for the seven species were estimated based on the description of habitat use of different species by Marttila et al. (2000).

Species-specific mobility estimates of Komonen et al. (2004) were average values of independent estimates on a scale of 0–10 received from 13 experienced Finnish lepidopterists. The average values for our 67 focal species varied from 1.6 to 8.8. We classified the mobility values published by Komonen et al. into four mobility classes (cf. Maes and van Dyck 2001): 1 (including earlier values 1.6–2.9) = very low ($n = 9$), 2 (3.0–4.9) = low ($n = 21$), 3 (5.0–6.9) = moderate ($n = 28$) and 4 (≥7.0) = high ($n = 16$) mobility. The seven species with missing values were classified based on other published mobility classifications (Cowley et al. 2001; Maes and van Dyck 2001).

Nutrient status of the breeding habitat was measured with a three-class variable (1–3; 1 corresponding to low and 3 to high nutritional requirements of the larval host plants) using the estimates published by Maes and van Dyck (2001) for 37 of our focal species. For 10 species we slightly modified the classification of Maes and van Dyck to fit their classification to the ecology of these species in Finland. For the other 27 species we estimated the nutrient status of the breeding habitat based on the Ellenberg values (Ellenberg et al. 2001) of their larval host plants in Finland (Huldén et al. 2000) and additional ecological literature (e.g. Marttila et al. 2000) following the methodology of Maes and van Dyck (2001). For 4 Hesperiidae and 11 Satyrinae species with grass-feeding larvae, but insufficient knowledge on the used host plant species, we made the classification based on observed habitat use of the adult butterflies in Finland (Marttila et al. 2000; M. Kuussaari and J. Heliölä, unpublished).

Information on overwintering stage (egg, larva, pupa or adult) and larval host plants was based on Huldén et al. (2000). Larval host plants were classified into three groups: woody, grassy and herbaceous.

Results

Variation in atlas data quality

Comparison of the distributions of the records in six rarity classes revealed differences in data quality between the four study periods (Fig. 2). Common species tended to be under-represented and rare species over-represented in the old data compared to the more recent data. For example, during the first two recording periods species of the rarest rarity class represented 0.20–0.36% of all the records on average, whereas in the last two study periods the corresponding proportion was only 0.05% of all the records. Before 1960

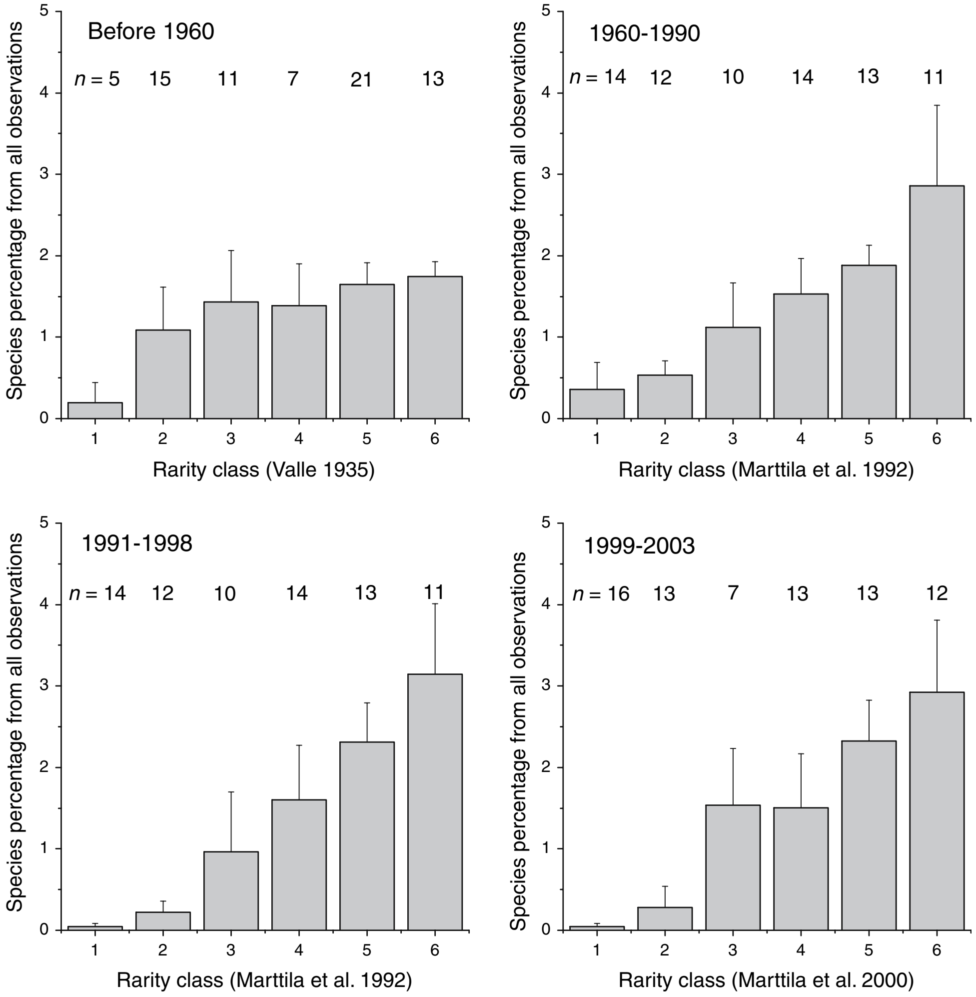

Fig. 2 Distribution of observations of the 74 butterfly species divided into six rarity classes during each of the four time periods. Within each rarity class the bar shows the mean percentage (+standard error) of observations per one species from all observations for the time period. The numbers above the bars indicate the numbers of species within each rarity class. Two species *(Lycaena dispar* and *Araschnia levana*) were first recorded in Finland after 1960. They are, therefore, not included in the first panel. See text for more details

there were almost as many records of intermediately rare species as of the most common species. In contrast, during the two most recent recording periods the two commonest species classes constituted a substantially larger proportion of records than the rarer classes.

Effect of study effort on observed trends in occupancy

Four datasets with varying minimum study effort (measured as the total number of butterfly records per study square) per study period produced differing, sometimes even contrasting, trends in occupancy. Spurious, strongly increasing trends were found especially in common species when the trends were based on all existing data, including study squares with only a few observations per study period. Such trends tended to disappear when the trend was based on the better studied 10 km squares. Figure 3 shows representative examples of trends in one very common, one relatively common and one rare species. *Pieris napi*, the most common butterfly species in Finnish agricultural landscapes, showed a strong increasing trend based on all records, but close to stable occupancy of 10 km squares based only on well-surveyed squares. The more restricted *Lycaena hippothoe* showed a slightly increasing trend based on all records, but a decreasing trend based on the best-studied squares. In the rare species *Cupido minimus* the rate of decline was lowest when based on all records and strongest when based on the best-surveyed squares.

Occupancy trends in 10 km squares

Observed changes in the occupancy of well-studied 10 km squares are shown separately for the species of arable field margins, semi-natural grasslands and forest edges in Tables 2, 3 and 4, respectively. A statistically significant trend (*F*-test, $P < 0.05$) was detected in 86% of the species (Tables 2–4). Figure 4

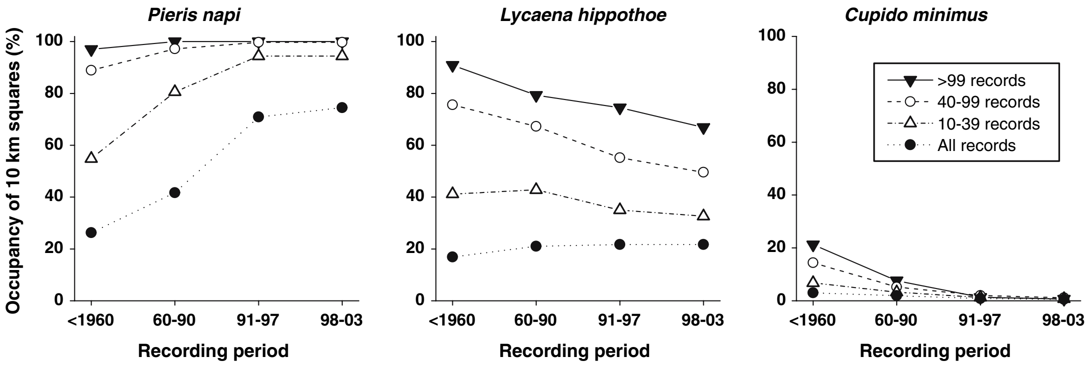

Fig. 3 Trends of selected common (*Pieris napi*), intermediately rare (*Lycaena hippothoe*) and rare (*Cupido minimus*) butterfly species based on four datasets with differing sampling efforts (including the 10 km squares with ≥1, ≥10, ≥40 and ≥100 records of the 74 focal species during each time period)

Table 2 Trends in occupancy in the species preferring arable field margins[a]

Species	Long-term trend in well-studied squares (n = 141)						Trend class
	Occupancy (%)				GLMM model		
	<1960 n = 90	1960–1990 n = 97	1991–1998 n = 95	1999–2003 n = 100	Complexity	P-value	
Pieris brassicae[b]	82.2	79.4	80.0	83.0	–	ns	0
Pieris rapae[b]	71.1	66.0	65.3	88.0	3	<0.0001	+
Pieris napi	88.9	94.8	100.0	100.0	3	<0.0001	+
Nymphalis urticae	87.8	90.7	98.9	99.0	3	<0.0001	+
Nymphalis io	35.6	77.3	82.1	93.0	3	<0.0001	+
Vanessa atalanta[b]	71.1	76.3	90.5	96.0	2	<0.0001	+
Vanessa cardui[b]	75.6	78.4	92.6	86.0	3	<0.0001	+

[a] GLMM model complexity indicates the order (first, second or third) of the model with the best fit to the data. Trend classes: 0 = stable, + = increasing

[b] Four common and regularly observed migratory species were included in the butterfly species of Finnish agricultural landscapes because their numbers often constitute a substantial proportion of butterfly individuals especially in field margins during the late summer (M. Kuussaari and J. Heliölä, unpublished). These species typically migrate to Finland during the early summer and produce a more numerous native generation which flies in their Finnish breeding habitat during the late summer

shows examples of fitted generalized linear models describing the observed trends in occupancy. Based on the statistical models and the observed changes in the occupancy, the 74 species were classified into four trend categories (Tables 2–4): declining (23), stable (17), increasing (27) and fluctuating (7 species). The class of fluctuating species was needed because in seven species we found a similar fluctuating trend: first a clear decline and then, in recent years, a clear increase (e.g. in *Aporia crataegi*, *Limenitis populi* and *Thecla betulae*; Fig. 4).

Many of the declining species had disappeared from more than half of the study squares. Two species (*Maniola lycaon* and *Lasiommata megera*) had become nationally extinct and seven others (e.g. *Hesperia comma*, *Lycaena helle*, *Boloria titania* and *Melitaea diamina*) had disappeared from >80% of their former distribution area. In all three habitats there were also species, which had significantly increased their occupancy. Although statistically significant, these tended to be relatively slight increases of already previously common species such as *Gonepteryx rhamni*, *Brenthis ino*, *Aphantopus hyperantus* and *Lasiommata maera*. A more substantial increase in occupancy with a northward expansion was observed in *Nymphalis io* (from 36% to 93% occupancy) and *Araschnia levana* (from 0% to 22% occupancy).

Differing trends according to habitat preference

Trends in occupancy differed significantly between the species groups preferring different habitats (Kruskal–Wallis test, $H = 15.0$, df = 66, $P < 0.001$; Fig. 5). Pair-wise comparisons showed that trends in

Table 3 Trends in occupancy in the species preferring semi-natural grasslands[a]

Species	Long-term trend in well-studied squares (n = 141)						Trend class	Recent trend	
	Occupancy (%)				GLMM model			Occupancy (%)	
	<1960 n = 90	1960–1990 n = 97	1991–1998 n = 95	1999–2003 n = 100	Complexity	P-value		1991–1998 n = 210	1999–2003 n = 210
Pyrgus malvae	81.1	72.2	65.3	62.0	1	<0.0001	–		
Pyrgus alveus	62.2	33.0	17.9	17.0	1	<0.0001	–		
Thymelicus lineola	61.1	84.5	96.8	98.0	3	<0.0001	+		
Hesperia comma	48.9	16.5	7.4	7.0	3	<0.0001	–		
Parnassius apollo	33.3	7.2	5.3	7.0	2	<0.0001	–		
Parnassius mnemosyne	24.4	13.4	6.3	9.0	1	<0.0001	–		
Lycaena phlaeas	80.0	77.3	81.1	88.0	2	<0.0001	0		
Lycaena helle	34.4	4.1	1.1	1.0	3	<0.0001	–		
Lycaena dispar[b]	0.0	3.1	2.1	4.0	Model not converged		+		
Lycaena virgaureae	88.9	81.4	95.8	97.0	3	<0.0001	+		
Lycaena hippothoe	75.6	69.1	60.0	65.0	1	0.0258	–	58.6	56.2
Cupido minimus	14.4	7.2	3.2	2.0	1	<0.0001	–		
Scolitantides orion	21.1	11.3	3.2	4.0	3	<0.0001	–		
Glaucopsyche alexis	46.7	42.3	13.7	14.0	3	<0.0001	–		
Aricia artaxerxes	53.3	58.8	52.6	63.0	–	ns	0		
Aricia nicias	11.1	7.2	6.3	6.0	2	0.0026	–	8.1	5.7
Aricia eumedon	56.7	47.4	47.4	48.0	–	ns	0		
Polyommatus semiargus	78.9	81.4	88.4	93.0	1	<0.0001	+		
Polyommatus amandus	78.9	86.6	89.5	95.0	1	<0.0001	+		
Polyommatus icarus	75.6	74.2	81.1	88.0	1	0.0017	+	78.1	82.9
Argynnis aglaja	80.0	80.4	87.4	92.0	2	<0.0001	+		
Argynnis niobe	56.7	46.4	38.9	33.0	1	<0.0001	–		
Argynnis adippe	74.4	81.4	83.2	86.0	1	<0.0001	+		
Issoria lathonia	77.8	44.3	13.7	17.0	3	<0.0001	–		
Brenthis ino	83.3	85.6	91.6	94.0	1	<0.0001	+		
Boloria selene	82.2	92.8	92.6	91.0	2	0.0011	0		
Melitaea cinxia	16.7	6.2	9.5	6.0	1	<0.0001	–		
Melitaea diamina	18.9	4.1	1.1	2.0	3	<0.0001	–		
Euphydryas aurinia	18.9	14.4	5.3	6.0	3	<0.0001	–		
Maniola jurtina	77.8	35.1	12.6	17.0	3	<0.0001	–		
Hyponophele lycaon	3.3	1.0	0.0	0.0	3	<0.0001	–		
Aphantopus hyperantus	85.6	89.7	93.7	98.0	3	<0.0001	+		
Coenonympha pamphilus	85.6	68.0	65.3	59.0	1	<0.0001	–		
Coenonympha glycerion	66.7	70.1	53.7	58.0	3	<0.0001	–	46.7	44.3
Lasiommata megera	2.2	0.0	0.0	0.0	3	<0.0001	–		

[a] GLMM model complexity indicates the order (first, second or third) of the model with the best fit to the data. Trend classes: – = declining, 0 = stable, + = increasing. Occupancy in the larger set of well-surveyed 10 km squares during the last two study periods is shown for those species for which the trend classification was difficult to apply based only on the primary set of data from the four study periods

[b] In the classification by Pitkänen et al. (2001) *Lycaena dispar* was considered as a species of field margins, farmyards and "wastelands", because some of its recent new populations in Finland were found on wastelands (e.g. in former dumping areas) close to urban areas. Here we decided to reclassify it as a species of semi-natural grasslands because its populations in Finnish agricultural landscapes tend to occur in moist meadows

the species of semi-natural grasslands differed from the trends in the species of field margins and forest edges ($P < 0.05$), but trends in the latter two groups did not differ from each other ($P > 0.05$). In the species of semi-natural grasslands ($n = 35$), decline was the prevailing trend (60% of the species). In contrast, all but one species of field margins ($n = 7$) had increased. In the species of forest edges ($n = 32$), increase (11 species) rather than decrease (2 species) was also the prevailing trend. Including the seven fluctuating species with a clear recent increase (Table 4), a total of 56% of the forest species demonstrated an increasing trend.

Occupancy trends and other species traits

There were significant differences in three of the four studied ecological characteristics between decreasing and increasing species. Average habitat

Table 4 Trends in occupancy in the species preferring forest edges and clearings[a]

Species	Long-term trend in well-studied squares (n = 141)						Trend class	Recent trend	
	Occupancy (%)				GLMM model			Occupancy (%)	
	<1960 n = 90	1960–1990 n = 97	1991–1998 n = 95	1999–2003 n = 100	Complexity	P-value		1991–1998 n = 210	1999–2003 n = 210
Carterocephalus palaemon	17.8	14.4	15.8	11.0	3	<0.0001	0	22.9	24.8
Carterocephalus silvicola	61.1	64.9	58.9	64.0	–	ns	0		
Ochlodes venatus	85.6	84.5	95.8	96.0	2	<0.0001	+		
Papilio machaon	84.4	69.1	69.5	67.0	2	<0.0001	0		
Leptidea sinapis	83.3	84.5	78.9	92.0	3	<0.0001	F	85.2	92.9
Aporia crataegi	83.3	47.4	56.8	69.0	2	<0.0001	F		
Anthocaris cardamines	80.0	85.6	87.4	92.0	1	<0.0001	+		
Gonepteryx rhamni	86.7	85.6	95.8	98.0	3	<0.0001	+		
Thecla betulae	36.7	21.6	13.7	30.0	3	<0.0001	F		
Quercusia quercus	11.1	20.6	17.9	19.0	2	0.0002	0		
Satyrium w-album	0.0	4.1	3.2	5.0	Model not converged		+		
Fixsenia pruni	32.2	30.9	21.1	32.0	3	0.0025	F	16.7	26.7
Callophrys rubi	81.1	86.6	91.6	96.0	1	<0.0001	+		
Celastrina argiolus	73.3	84.5	84.2	83.0	1	0.0126	0		
Plebejus argus	87.8	74.2	80.0	88.0	2	0.0001	0	84.3	88.1
Plebejus idas	71.1	74.2	80.0	74.0	–	ns	0		
Apatura iris	6.7	5.2	2.1	9.0	3	<0.0001	F	1.0	6.7
Limenitis populi	72.2	25.8	11.6	28.0	3	<0.0001	F		
Nymphalis antiopa	77.8	88.7	95.8	98.0	1	<0.0001	+		
Polygonia c-album	85.6	80.4	93.7	93.0	3	<0.0001	+	92.4	92.9
Araschnia levana	0.0	2.1	1.1	22.0	1	<0.0001	+		
Argynnis paphia	62.2	30.9	23.2	35.0	2	<0.0001	F	19.0	38.6
Boloria thore	1.1	3.1	2.1	2.0	2	<0.0001	0		
Boloria titania	41.1	11.3	3.2	2.0	1	<0.0001	–		
Boloria euphrosyne	78.9	80.4	84.2	86.0	1	<0.0001	+		
Mellicta athalia	81.1	73.2	72.6	80.0	–	ns	0	76.7	80.5
Hypodryas maturna	37.8	40.2	28.4	34.0	3	<0.0001	0	34.3	40.0
Erebia ligea	70.0	74.2	84.2	78.0	3	<0.0001	+	85.2	86.2
Pararge aegeria	58.9	59.8	55.8	63.0	–	ns	0		
Lasiommata maera	78.9	74.2	87.4	91.0	2	<0.0001	+		
Lasiommata petropolitana	72.2	69.1	65.3	62.0	–	ns	0	71.0	71.0
Lopinga achine	37.8	16.5	2.1	3.0	3	<0.0001	–		

[a] GLMM model complexity indicates the order (first, second or third) of the model with the best fit to the data. Trend classes: – = declining, 0 = stable, + = increasing, F = fluctuating. Occupancy in the larger set of well-surveyed 10 km squares during last two study periods is shown for those species for which the trend classification was difficult based only on the primary set of data from the four study periods

breadth, nutrient status of the breeding habitat and mobility were all higher in increasing than in decreasing species (Table 5). However, these traits were not independent from each other, since all the three traits were significantly positively correlated with each other (Spearman's rank correlation coefficients 0.49–0.58, $P < 0.05$, $n = 50$). Decreasing and increasing species did not differ significantly in host specificity, although there was some tendency for increasing species to be more polyphagous on average than decreasing species (Table 5). Host specificity was positively correlated with habitat breadth ($r_S = 0.29$, $P < 0.05$, $n = 50$).

Overwintering stage was the only categorical species trait in which a significant difference in average trend in occupancy was detected between the categories (Kruskal–Wallis test, $H = 9.73$, df = 66, $P = 0.02$). Pair-wise comparisons showed that average trend in occupancy was significantly more positive in species overwintering as adults than in species overwintering as eggs, larvae or pupae ($P < 0.05$), but there were no significant differences between the other three overwintering stages ($P > 0.05$; Fig. 6). There was no statistically significant difference in average occupancy trend between species differing in their larval host plant growth form (Fig. 6).

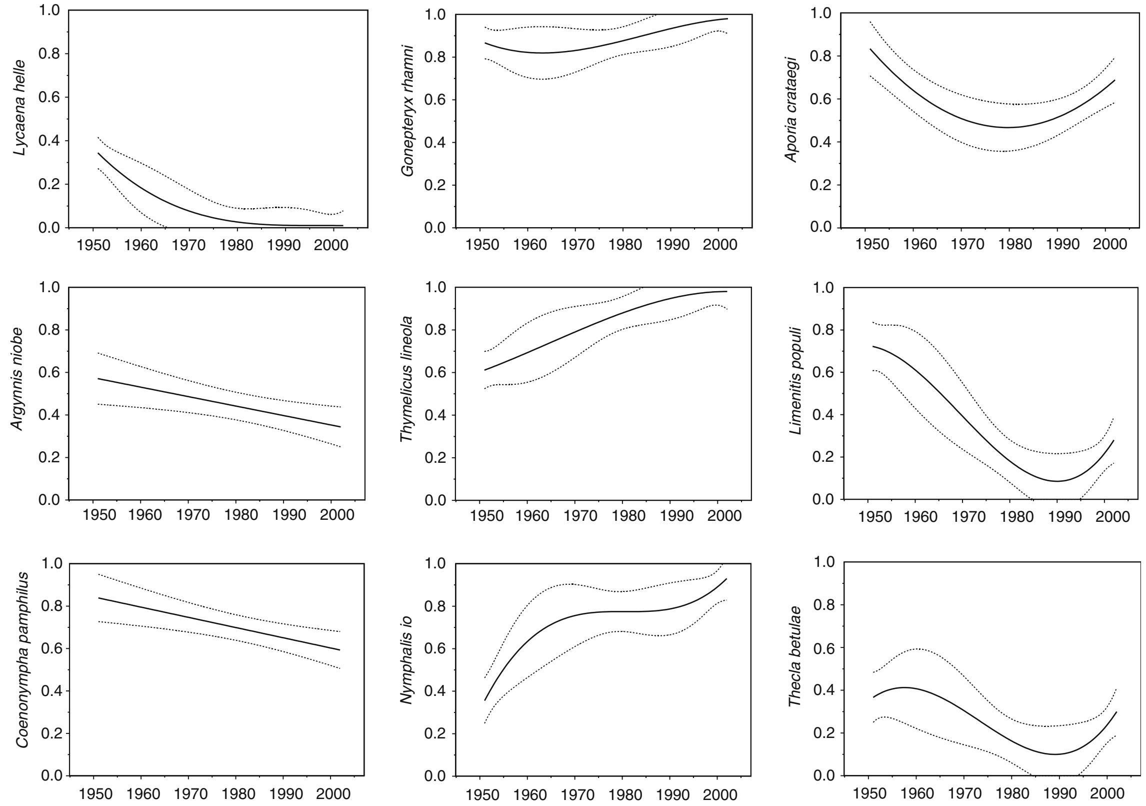

Fig. 4 Examples of fitted GLM (with the 95% confidence intervals for the fitted models) for selected declining, increasing and fluctuating butterfly species

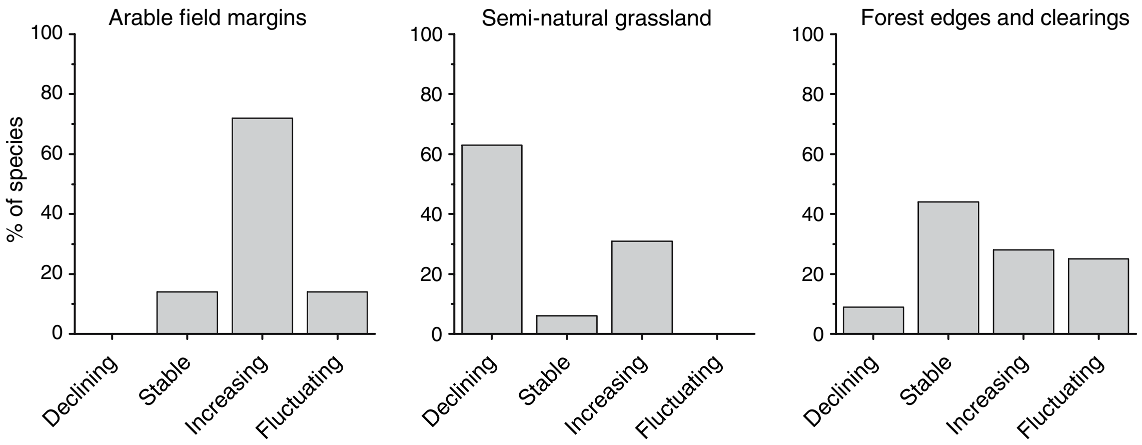

Fig. 5 Summary of long-term butterfly occupancy trends in the species of field margins (n = 7), semi-natural grasslands (n = 35) and forest edges (n = 32)

Discussion

Trends in occupancy and land use changes

Different occupancy trends between the species of semi-natural grasslands, arable field margins and forest edges are in a good agreement with the contrasting long-term changes in the availability of suitable habitat for grassland and forest edge species in Finland. This suggests that changes in land use are important drivers of the observed changes in butterfly occupancy of 10 km squares.

Table 5 Comparison of species traits between species with decreasing ($n = 23$) and increasing ($n = 27$) trends in occupancy

Variable	Declining species		Increasing species		*P*-value*
	n	Mean ± SD	*n*	Mean ± SD	
Host specificity	23	2.17 ± 0.94	27	2.48 ± 0.80	0.238
Habitat breadth	23	1.43 ± 0.93	27	2.44 ± 0.89	<0.001
Nutrient status of breeding habitat	23	1.39 ± 0.50	27	2.22 ± 0.58	<0.001
Mobility	23	1.87 ± 0.63	27	3.37 ± 0.74	<0.001

* Statistical significance based on Mann–Whitney *U*-test

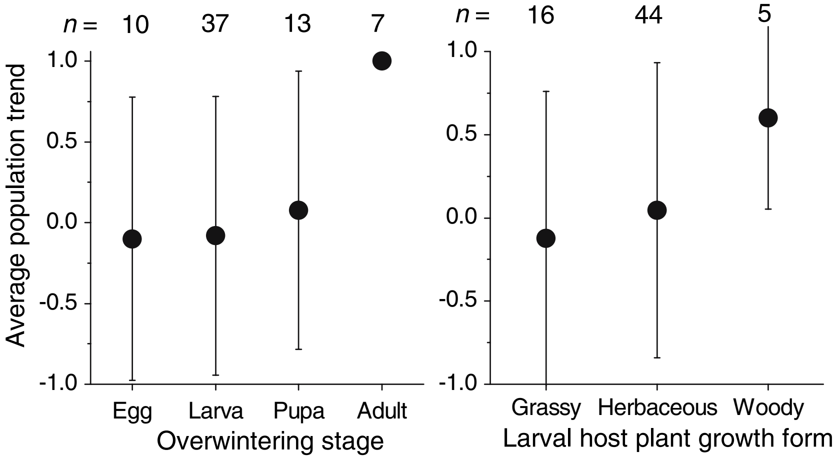

Fig. 6 Comparison of average occupancy trends (+standard errors) between butterflies with different overwintering stages and larval host plant growth forms

The decline by 60% of grassland species is not surprising because the area of semi-natural grasslands has continuously decreased for more than 100 years in Finland (Luoto et al. 2003). Luoto et al. (2003) showed that during the last ca 120 years >98% of the former semi-natural grasslands have been converted to arable land (mainly to intensive cereal and hay production) or have become overgrown to forests after the ceasing of cattle grazing. Abandonment of previously grazed natural pastures has probably contributed to both the decline and the increase of particular grassland species.

Empirical studies have shown that butterfly species richness tends to be highest in extensively grazed and recently abandoned semi-natural grasslands with intermediate vegetation height (Erhardt and Thomas 1991; Balmer and Erhardt 2000; Pöyry et al. 2006). Nevertheless, particular butterfly species may prefer either low or high vegetation heights. Pöyry et al. (2005) showed that the currently common grassland butterflies in Finland tend to be more abundant in ungrazed than in grazed semi-natural grasslands. This finding offers a plausible explanation for our observation that ten grassland butterflies have increased their occupancy despite the overall decline in the area of semi-natural grasslands. These species appear to have benefited from the increased proportion of abandoned semi-natural grasslands. All the four butterfly species which were most strongly associated with abandoned grasslands (*Polyommatus amandus*, *P. semiargus*, *Brenthis ino* and *Aphantopus hyperantus*) in the field studies of Pöyry et al. (2005) showed a consistent increase in their occupancy during our four study periods.

Pöyry et al. (2005) also showed that decreasing day-flying Lepidoptera, such as *Lycaena hippothoe* and *Camptogramma bilineatum*, tended to have positive associations with cattle-grazing, in contrast to many increasing species. This result and complementing results for other declining grassland species (e.g. *Maniola jurtina*, *Coenonympha pamphilus* and *Pyrgus malvae*) based on field surveys of grazed and abandoned semi-natural grasslands in the Åland islands (J. Heliölä, E.-L. Alanen and M. Kuussaari, unpublished), suggest that several of the declining Finnish butterflies have benefited from the traditional grazing management of semi-natural grasslands. Therefore, it is likely that the decline of many grassland species in Finland was caused by the decrease both in the area and the quality of semi-natural grasslands after the large-scale ceasing of cattle grazing on natural pastures. In contrast to some areas in Central Europe (e.g. Erhardt and Thomas 1991), increased fertilization and intensified use of semi-natural grasslands do not seem to have been major causes of butterfly decline in Finland.

The steep increase in the amount of open forest edges, clearings and small forest roads due to modern forestry is likely to have contributed to the increase of several forest edge species. Modern forestry practices, which were started in the 1950s (Punttila et al. 2005), have continuously produced new clear-cut areas, often with warm and sheltered microclimatic conditions at the forest edge. At the same time the amount of small forest roads in Finland has increased more than 20-fold, from ca 6,000 km in 1960 to ca 130,000 km in 2003 (Punttila et al. 2005). This network of occasionally used small forest roads offers a substantial amount of permanently suitable edge habitat and a dense network of potential movement corridors enhancing habitat connectivity for butterflies of open forest edges.

The fluctuating trends observed in seven forest edge species are likely to be associated with both climate and habitat availability. The fluctuating trends of *Argynnis paphia*, *Aporia crataegi* and *Limenitis populi*, in particular, were already noted some decades earlier (Kaisila 1962; Mikkola 1979, 1997). The recent expansion of several forest edge species during the climatically favourable years has been enabled by the good availability of suitable forest edges and clearings in terms of both habitat area and connectivity. In contrast, the fact that most grassland species have not been able to benefit from the favourable climatic conditions is probably associated with the current poor availability of semi-natural grasslands in Finland, a similar pattern, which previously has been reported for specialist butterflies in Britain (Warren et al. 2001).

Six of the seven species of open arable field margins showed increasing trends despite the long-term decline in the area of field margins in Finnish farmland (Hietala-Koivu 2003). These included four Nymphalid species with nettle-feeding caterpillars (*Nymphalis urticae*, *N. io*, *Vanessa atalanta* and *V. cardui*) and two Pierids (*Pieris napi* and *P. rapae*), the caterpillars of which feed on crucifers and may also breed in cultivated fields. All these species may have benefited from the increasing eutrophication of farmland due to the increased use of chemical fertilizers and atmospheric nitrogen deposition (see Oostermeijer and van Swaay 1998; Öckinger et al. 2006). *N. io*, which has recently expanded northwards, as well as the three migratory species *P. rapae*, *V. atalanta* and *V. cardui*, have probably also benefited from the warming climate (Sparks et al. 2005).

The Finnish butterfly trends have both similarities and differences when compared to trends reported from other European countries. Our results fit the emerging general view that decline of grassland butterflies is a European-wide problem (van Swaay and Warren 1999; van Swaay and van Strien 2005; van Swaay et al. 2006), which has been highlighted by several detailed studies on various spatial scales in many countries (e.g. Maes and van Dyck 2001; Warren et al. 2001; Öckinger et al. 2006; Wenzel et al. 2006). On the other hand, relatively few European studies have reported increases of butterflies, although several recent studies have associated the observed increasing trends and expansions of butterflies in their northern ranges to climate change (Parmesan et al. 1999; Thomas et al. 2001; Warren et al. 2001; Hill et al. 2002; Davies et al. 2005). The pattern of contrasting trends in species of different habitats, which we found in Finland, resembles the pattern previously reported for British butterflies (Hill et al. 1999, 2002; Warren et al. 2001): several species with a relatively good habitat availability are increasing, whereas many species with poor habitat availability continue to decrease despite the currently favourable climatic conditions. The observed large-scale increase of forest edge species in Finland appears rather exceptional when compared with studies on butterfly trends in other parts of Europe.

Occupancy trends and atlas data

Our results show that analyses of atlas data may produce spurious increasing (but not decreasing) trends in occupancy when selective recording is combined with spatially and temporally varying study effort. Common butterfly species were often not recorded in 10 km squares with a small number of old records, seemingly because recording was biased towards rare species. In the analyses we minimised these problems by focusing only on the 10 km squares, which were well surveyed during at least two study periods. The example of *Pieris napi* in Fig. 2 suggests that some additional increasing trends of common species might have disappeared if a higher recording effort had been used for the first two study periods. In other words, our results may somewhat overestimate the number of increasing trends of common species which tended to be under-recorded during the first two study periods, before 1960 and in 1960–1990. It should be noted, however, that in several cases the increasing trend continued during the last two study periods, which had more systematic recording of all butterfly species within the 10 km squares. Furthermore, the under-recording of common species in the old data cannot explain the observed contrasting trends of the species of different habitats. Therefore the relative differences in the observed trends between species are probably true.

Also the spatial scale of species surveys has been shown to influence the probability of detecting declines of species distribution areas. Based on earlier studies by Thomas and Abery (1995) and Cowley et al. (1999) it is likely that our surveys which were conducted in the relatively coarse scale of 10 km squares underestimate the actual number of declining species and the actual extent of their decline in Finland. With high quality survey data in a smaller spatial scale (e.g. in 1 or 5 km square) from the same study areas we would expect to reveal higher rates of decline than observed in the current study.

Species traits associated with trends in occupancy

Four of the six studied species traits were associated with changes in distribution area. Increasing species were more mobile, utilized a wider range of habitats and, based on their larval host plants, lived in more eutrophic habitats than declining species. In contrast, declining species were more sedentary, more specialized in their habitat use and tended to occur in more oligotrophic habitats than increasing species. It is important to recognize, however, that these three traits are interrelated and cannot be considered as independent traits. Differences between increasing and declining species appear to have some generality, because other recent butterfly studies conducted in Belgium (Maes and van Dyck 2001), Germany (Wenzel et al. 2006) and Sweden (Öckinger et al. 2006) have reported very similar results. The results of Kotiaho et al. (2005) for threatened versus other butterfly species in Finland are also in agreement with our results. We also found that species overwintering as adults showed more positive trends in occupancy than species overwintering as eggs, larvae or pupae. This comparison appears not to have been considered by previous studies on the relationships between species traits and population trends. One possibility is that species overwintering as adults may have benefited from warming average spring temperatures (Tuomenvirta 2004) more than other species.

Use of indicator classifications in conservation

The identification of butterflies living in boreal agricultural landscapes and their division into species of three common habitats and four occupancy trend classes offer useful indicator classifications for monitoring studies. Such indicator classifications can be used as tools for monitoring the success of practical conservation management, because they help to focus on the species groups especially in need of attention. For example, it may be useful to concentrate on declining grassland butterflies in studies of management of semi-natural grasslands. On a European level, there is considerable scope for the use of indicator classifications of farmland species in studies monitoring the effects of agri-environment schemes (Kleijn et al. 2006). Habitat preferences and trends in species occurrence and abundance are likely to be among the most potential species characteristics in developing practical indicator classifications.

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Appendix Summary of the six species traits for the 74 butterfly species of Finnish agricultural landscapes. See Material and methods for explanation of trait classes.

Species	Host specificity	Habitat breadth	Nutrient status	Mobility	Overwintering stage	Host plant growth form
Hesperiidae						
Pyrgus malvae	3	2	1	2	Pupa	Herbaceous
Pyrgus alveus	3	2	1	2	Egg	Herbaceous
Carterocephalus palaemon	3	1	2	2	Larva	Grassy
Carterocephalus silvicola	3	1	2	3	Larva	Grassy
Thymelicus lineola	3	3	2	3	Egg	Grassy
Hesperia comma	3	1	1	2	Egg	Grassy
Ochlodes sylvanus	3	3	2	3	Larva	Grassy
Papilionidae						
Parnassius apollo	1	1	1	2	Egg	Herbaceous

Appendix continued

Species	Host specificity	Habitat breadth	Nutrient status	Mobility	Overwintering stage	Host plant growth form
Parnassius mnemosyne	1	1	2	2	Egg	Herbaceous
Papilio machaon	3	3	2	4	Pupa	Herbaceous
Pieridae						
Leptidea sinapis	3	1	2	3	Pupa	Herbaceous
Aporia crataegi	3	1	2	3	Larva	Woody
Pieris brassicae	3	3	3	4	Pupa	Herbaceous
Pieris rapae	3	3	3	4	Pupa	Herbaceous
Pieris napi	3	4	3	4	Pupa	Herbaceous
Anthocharis cardamines	3	3	2	4	Pupa	Herbaceous
Gonepteryx rhamni	2	4	2	4	Adult	Woody
Lycaenidae						
Thecla betulae	1	2	2	2	Egg	Woody
Favonius quercus	1	2	2	1	Egg	Woody
Satyrium w-album	1	1	2	1	Egg	Woody
Satyrium pruni	1	2	2	2	Egg	Woody
Callophrys rubi	3	2	1	3	Pupa	Herbaceous
Lycaena phlaeas	2	3	1	3	Larva	Herbaceous
Lycaena helle	1	1	1	2	Pupa	Herbaceous
Lycaena dispar	2	2	2	3	Larva	Herbaceous
Lycaena virgaureae	1	3	2	3	Egg	Herbaceous
Lycaena hippothoe	1	1	2	2	Larva	Herbaceous
Cupido minimus	3	1	1	1	Larva	Herbaceous
Celastrina argiolus	3	2	2	3	Pupa	Woody
Scolitantides orion	1	1	1	1	Pupa	Herbaceous
Glaucopsyche alexis	3	2	2	2	Pupa	Herbaceous
Plebeius argus	3	2	1	3	Egg	Herbaceous
Plebeius idas	3	2	1	3	Egg	Herbaceous
Aricia artaxerxes	2	1	2	2	Larva	Herbaceous
Aricia nicias	1	1	2	2	Larva	Herbaceous
Aricia eumedon	1	2	2	2	Larva	Herbaceous
Polyommatus semiargus	3	2	2	3	Larva	Herbaceous
Polyommatus amandus	3	3	2	3	Larva	Herbaceous
Polyommatus icarus	3	1	2	3	Larva	Herbaceous
Nymphalidae						
Apatura iris	2	1	2	3	Larva	Woody
Limenitis populi	2	1	2	4	Larva	Woody
Nymphalis antiopa	3	2	2	4	Adult	Woody
Nymphalis io	1	3	3	4	Adult	Herbaceous
Vanessa atalanta	3	3	3	4	Adult	Herbaceous
Vanessa cardui	3	3	3	4	Adult	Herbaceous
Nymphalis urticae	1	3	3	4	Adult	Herbaceous
Nymphalis c-album	3	3	3	4	Adult	Herb./Woody
Araschnia levana	1	2	3	2	Pupa	Herbaceous
Argynnis paphia	2	2	2	3	Larva	Herbaceous
Argynnis aglaja	2	1	2	4	Larva	Herbaceous
Argynnis niobe	2	1	1	3	Larva	Herbaceous
Argynnis adippe	2	2	2	4	Larva	Herbaceous
Issoria lathonia	2	2	2	3	Larva	Herbaceous
Brenthis ino	3	2	2	3	Larva	Herbaceous
Boloria selene	2	2	2	3	Larva	Herbaceous
Boloria thore	2	1	2	1	Larva	Herbaceous
Boloria titania	2	1	2	1	Larva	Herbaceous
Boloria euphrosyne	3	3	1	4	Larva	Herbaceous
Melitaea cinxia	3	1	1	2	Larva	Herbaceous
Melitaea diamina	1	1	2	1	Larva	Herbaceous
Melitaea athalia	3	1	1	3	Larva	Herbaceous
Euphydryas maturna	3	1	1	3	Larva	Herb./Woody
Euphydryas aurinia	1	1	1	2	Larva	Herbaceous

Appendix continued

Species	Host specificity	Habitat breadth	Nutrient status	Mobility	Overwintering stage	Host plant growth form
Satyrinae						
Erebia ligea	3	1	2	3	Larva	Grassy
Maniola jurtina	3	1	1	2	Larva	Grassy
Maniola lycaon	3	1	1	2	Larva	Grassy
Aphantopus hyperantus	3	3	2	3	Larva	Grassy
Coenonympha pamphilus	3	3	1	2	Larva	Grassy
Coenonympha glycerion	3	1	2	1	Larva	Grassy
Pararge aegeria	3	1	2	2	Pupa	Grassy

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