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The Number of Butterfly Species in Woodlands

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Summary. The number of butterfly species present in 22 woods in eastern England was recorded during fortnightly visits between May to October 1978. A total of 26 species was observed. The number of species present was significantly correlated with the area of woodland but not with the area of glades and rides, which provided both larval food plants and adult foraging sites. The number of vagile species, but not the number of poorly vagile species, present was correlated with the area of woodland within 1 km of the study wood, this being a measure of the sources of potential colonizers. It was predicted that a woodland area of about 460 ha would be required to support all the species recorded in the study.

Introduction

Agricultural developments over the last thirty years have resulted in a rapid change in the landscape of the eastern counties of England, with a reduction in the number of hedges (Pollard et al., 1974) and in the area of permanent grassland, heathland and scrub (Ratcliffe, 1977). This has decreased the area of suitable habitat available to many species of plants and animals and has increased the isolation of those species living in woodland. The relationship between the number of butterfly species and the area and isolation of their woodland habitat in eastern England is examined in the present paper.

Methods

Twenty-two woods in north-east Essex and south Suffolk were selected for variety in area and management regime. Each site was visited once every 14 days from 9th May to 2nd October, 1978. Species were recorded using transect counts (Pollard, 1977). The time spent on individual transects varied from 2 h 30 min in the largest wood (area 175 ha) to 30 min in the smallest wood (area 2 ha). Management was recorded by observing current usage on the first visit to each wood. Measurements of the area of sites, when not available from records, and of the area and number of woods surrounding each site were taken from 1:25,000 Ordnance Survey sheets.

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Results

The site descriptions are summarised in Table 1. With the exception of Dodnash Wood, Layer Wood and Pods Wood the sites were situated on boulder clay. Dodnash Wood was on silty drift, Layer Wood and Pods Wood were on sand.

Nine sites were conifer plantations which had been planted since 1955 on areas of cleared, mixed deciduous woodland. Six sites were coppiced woodland, three of which were commmercially managed chestnut (*Castanea sativa*) coppices, the remaining three being managed as mixed coppice to preserve their flora and fauna. The remaining seven sites were unmanaged, mixed deciduous woodland.

Six of the eight largest woods (area $\geqq 50$ ha) were coniferised, one was unmanaged and one coppiced. Of the six medium sized sites (area 30–47 ha) four were coppiced and two were coniferised. Six of the eight small sites (area $\leqq 23$ ha) were unmanaged, one was coniferised and one coppiced.

Twenty-six species of butterflies were recorded and their distribution is given in Table 2. The most widespread species were *Pieris napi* (22 sites), *Pieris brassicae* (20 sites) and *Pieris rapae* (20 sites). The least widespread species were *Aricia agestis* (1 site), *Ladoga camilla* (2 sites) and *Argynnis paphia* (2 sites).

The number of species at each site showed no correlation with glade and ride area (Spearman rank correlation; $r_s = 0.199$; $P > 0.1$) but was significantly correlated with total woodland area ($r_s = 0.729$; $P < 0.001$). The relationship between area and the number of species is shown in Fig. 1. At two sites, only 1 species was found. Omitting these sites from the analysis, the number of species at the remaining 20 sites was still significantly correlated with total woodland area ($r_s = 0.649$; $P < 0.005$) but again showed no correlation with glade and ride area ($r_s = 0.126$; $P > 0.1$).

Two models which may account for this relationship are:

$\log S = \log k + z \log A$
(a double logarithmic transformation of a power function)

or $S = \log k + z \log A$
(derived from an exponential function)

where S = species number, A = woodland area, k and z are constants.

The regressions of the number of species against area using both model formulae are given in Table 3. The correlation coefficients (r) of these two models differ by 5%.

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Table 1. Descriptions of woodland study areas

	Site name	Grid references	Area		Isolation				Management				S
			1	2	3	4	5	6	7	8	9	10	
1	Markshall Wood	TL 8426	175	4.85	4	94	10	107	+				18
2	Lineage Wood	TL 8848	85	2.37	5	9	9	27	+				22
3	Shardlowes Wood	TL 7831	80	3.25	4	24	4	24	+				17
4	Hintlesham Great Wood	TM 0743	70	0.15	3	4	6	38		+			15
5	Stour Wood	TM 1831	65	0.72	4	44	5	47			+		15
6	Assington Thicks	TL 9237	58	1.05	1	2	10	38	+				20
7	Pods Wood	TL 9017	55	1.0	5	73	6	75	+				15
8	Layer Wood	TL 9118	50	0.92	1	55	3	57	+				15
9	Bentley Hall Wood	TM 1124	47	12.0	2	5	5	14			+	+	18
10	Wolves Wood	TM 0543	40	0.7	1	2	2	72			+		19
11	Coperass Wood	TM 1931	39	0.07	1	65	1	65			+		20
12	Weeley Hall Wood	TM 1521	37	1.15	1	2	4	18			+		11
13	Dodnash Wood	TM 1036	35	4.5	6	60	9	72	+			+	11
14	Arger Fen	TL 9335	30	0.25	4	20	8	68	+				17
15	Bulls Cross Wood	TL 9544	23	1.25	4	16	10	22		+			8
16	Groton Wood	TL 9743	19	1.75	1	2	2	3			+		10
17	Hazel Wood	TL 9444	8	1.1	3	33	7	43		+			10
18	Wrights Wood	TL 9235	7	0.75	3	7	7	48	+				16
19	Long Wood	TL 9445	6	0.8	2	10	4	37		+			1
20	Walding Wood	TL 9444	4	0.2	2	31	5	42		+			6
21	Corner Place	TM 1223	3	0.05	0	0	4	7		+			10
22	Stattles Wood	TL 9445	2	0.25	1	6	3	16		+			1

Area 1 – Total woodland area (ha)
2 – Area of open vegetation (ha)

Isolation 3 – No. of woods within ½ km of site boundary
4 – Area of woods within ½ km of site boundary (ha)
5 – No. of woods within 1 km of site boundary
6 – Area of woods within 1 km of site boundary (ha)

Management 7 – Conifer plantation
8 – Unmanaged deciduous woodland
9 – Coppiced woodland
10 – Clear fell

S – No. of butterfly species recorded

The only measure of isolation, given in Table 1, with which the number of species is significantly correlated is the area of woodland within 1 km of the site boundary ($r_s=0.378$; $P<0.05$). A regression of species number against this measure of isolation gives:

$$\log S = 0.72 + 0.21 \log A$$

The gradient is significantly different from zero ($P<0.05$). This does not contribute significantly to a multiple regression of species number against site area and isolation.

The species in this study can be divided into two groups, vagile species whose occurrence at a site does not necessitate the presence of a breeding population, and poorly vagile species whose occurrence indicated the likelihood of a breeding population. The first group is composed of ten species, and the second group of sixteen species, indicated in Table 2. In both groups the number of species is significantly correlated with woodland area (vagile species, $r_s=0.750$, $P<0.001$; poorly vagile species, $r_s=0.631$, $P<0.005$), but shows no significant correlation with glade and ride area (vagile species, $r_s=0.194$, $P>0.1$; poorly vagile species, $r_s=-0.067$, $P>0.1$). The effect of area on these two groups is shown in Figs. 2 and 3. The regressions of the number of species against area for the two groups using both model formulae are given in Table 4. For both groups the correlation coefficients (r) of the two models differ by less than 5%.

The number of vagile species is not correlated with any of the measures of isolation given in Table 1. The number of poorly vagile species is correlated with the area of woodland within 1 km of the site boundary ($r_s=0.427$; $P<0.05$). A regression of the number of species against this measure of isolation gives:

$$\log S = 0.42 + 0.19 \log A$$

The gradient is significantly different from zero ($P<0.05$). This does not contribute significantly to a multiple regression of species number against area and isolation.

Table 2. The distribution of the twenty-six recorded species among the study sites

Species	Site number																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Thymelicus sylvestris Poda. Small skipper	+	+	+	+	+	+	+	+	+	+	+			+	+		+	+		+		
Thymelicus lineola Ochs. Essex skipper		+	+		+	+	+	+	+	+	+											
Ochlodes venata Br. and Grey. Large skipper	+	+	+	+	+	+	+	+	+	+	+	+		+							+	
Gonepteryx rhamni L. Brimstone *		+									+		+									
Pieris brassicae L. Large white*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	
Pieris rapae L. Small white*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	
Pieris napi L. Green-veined white*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Anthocharis cardamines L. Orange tip*	+	+	+	+		+	+		+	+	+		+	+		+	+	+			+	
Callophrys rubi L. Green hairstreak		+				+			+									+				
Quercusia quercus L. Purple hairstreak	+			+		+		+	+	+	+	+	+	+			+	+			+	
Strymonidia w-album Knoch. White-letter hairstreak		+								+								+				
Lycaena phlaeas L. Small copper	+	+	+	+		+	+	+	+	+	+		+	+		+	+	+			+	
Aricia agestis Schiff. Brown argus		+																				
Celastrina argiolus L. Holly blue	+		+	+	+	+	+		+	+	+	+	+	+		+						
Ladoga camilla L. White admiral			+		+																	
Vanessa atalanta L. Red admiral*	+	+				+			+		+											
Cynthia cardui L. Painted lady*		+										+										
Aglais urticae L. Small tortoiseshell*	+	+	+	+	+	+	+	+	+		+			+			+	+			+	
Inachis io L. Peacock*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+				
Polygonia c-album L. Comma*	+	+	+			+	+	+		+	+			+								
Argynnis paphia L. Silver-washed fritillary										+				+								
Lassiommata megera L. Wall brown	+	+		+	+	+		+	+	+	+							+			+	
Pyronia tithonus L. Gatekeeper	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+			+	
Maniola jurtina L. Meadow brown	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+		
Coenonympha pamphilus L. Small heath	+	+	+		+	+	+	+	+	+	+	+		+				+				
Aphantopus hyperantus L. Ringlet	+	+	+	+	+	+				+	+			+	+	+		+		+		

Nomenclature follows that of Kloet and Hincks (1972)
+ = species present
* = vagile species

Table 3. A comparison between two models which may account for the relationship between the number of butterfly species and woodland area

Model	Formula	r	$\log k$	z	F	P
log-normal	$\log S = \log k + z \log A$	0.71	0.34	0.50	20.9125	0.01
log-series	$S = C + K \log A$	0.76	1.44	8.51	28.6072	0.01

S = Species number; A = Woodland area (ha); k, z constants; r = correlation coefficient; F = value of 'F' for test of reduction of variance; P = significance of 'F' test

Table 4. A comparison between the relationships between the number of species and woodland area of vagile species and poorly vagile species

Group	Formula	r	$\log k$	z	F	P
Vagile species	$\log S = \log k + z \log A$	0.74	0.20	0.36	23.6626	0.01
Vagile species	$S = C + K \log A$	0.76	1.23	3.23	26.9458	0.01
Poorly vagile species	$\log S = C + K \log A$	0.64	0.50	0.26	12.6172	0.01
Poorly vagile species	$S = C + K \log A$	0.62	2.29	4.16	11.1223	0.01

S = Species number; A = Woodland area (ha); k, z constants; r = correlation coefficient; F = value of 'F' for test of reduction of variance; P = significance of 'F' test

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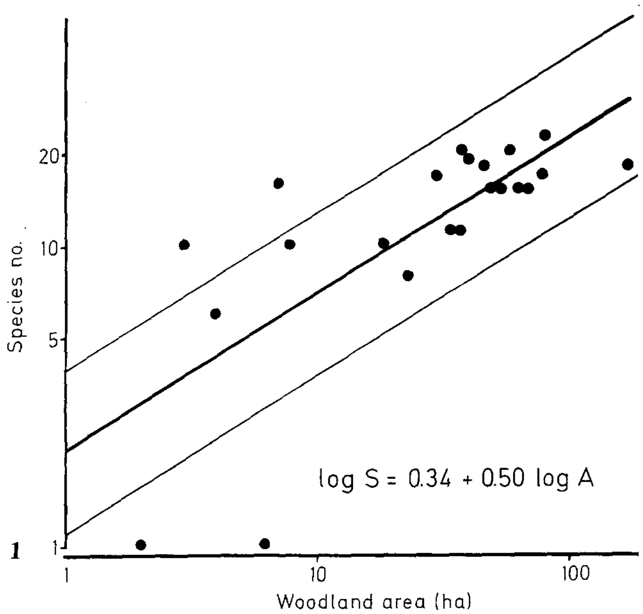

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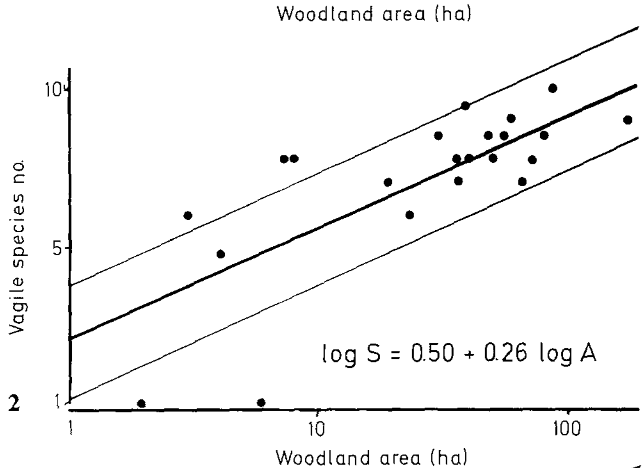

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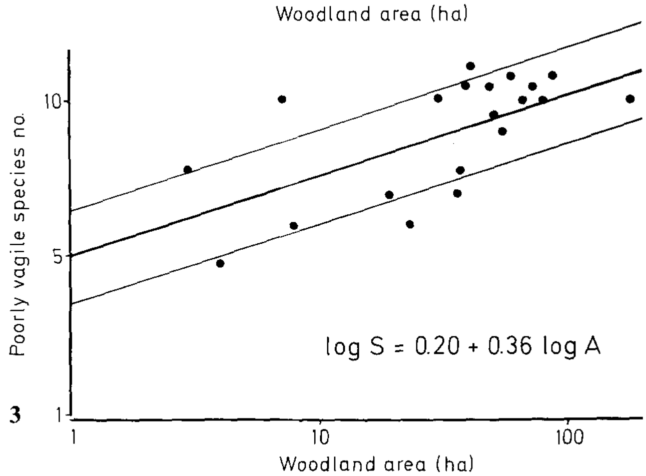

Fig. 1. The total number of butterfly species recorded in 22 woods. Fitted regression with 95% confidence limits

Fig. 2. The number of vagile species recorded in 22 woods. Fitted regression with 95% confidence limits

Fig. 3. The number of poorly vagile species recorded in 20 woods. Fitted regression with 95% confidence limits

Area alone accounts for 50% of the variation of the total number of species, for 54% of the variation of the number of vagile species and 40% of the variation of the number of poorly vagile species, when considered separately.

Discussion

The majority of butterfly species are not directly associated with woodland tree and shrub species but with the areas of open vegetation found in rides, glades and recent coppice working, these providing larval food plants and foraging sites for adults.

The extent of open vegetation within the study sites was related to both management and area. In unmanaged woodland the proportion of open areas was low and a natural glade pattern had not had time to develop since the last period of management. In both coppiced woodlands and conifer plantations the proportion of open areas was greater, increasing with the frequency of coppicing and decreasing with the age of the conifer stands. Most of the larger sites were coniferised, most of the medium sized sites were coppiced and the majority of the smaller sized sites were unmanaged. This is representative of current woodland usage in eastern England.

The commonest species of butterflies were highly mobile (Pieridae), or had widely distributed larval food resources (Satyridae). The least common species were either those with a localised larval food resource and poor adult dispersal ability (*Aricia agestis, Callophrys rubi, Strymonidia w-album*), or those which have recently declined in abundance throughout the eastern counties of England (*Ladoga camilla, Argynnis paphia*), their distribution being largely governed by climatic factors (Gilbert and Singer, 1975).

No correlation was demonstrated between the number of species and the area of open vegetation which provide food for larvae and adults, but there was a significant correlation between the number of species and total woodland area. Three alternative hypotheses can be advanced to account for this increase in species richness with area. Williams' (1964) habitat heterogeneity hypothesis describes the number of species in an area as a function of habitat diversity. An increase in sampling area increases the diversity of available habitats and species number increases with area as new habitats with their associated species are encountered. The island equilibrium model (MacArthur and Wilson, 1967) describes the number of species on an island as a dynamic equilibrium between immigration and extinction. The number of species on an island is dependent on its area and isolation, the distance from a source of immigrants. The third hypothesis states that species number is controlled by passive sampling from a species pool (Connor and McCoy, 1979), with larger areas receiving larger samples and hence more species than smaller areas. It denies the importance of habitat diversity, the role of immigration and the effects of area on species richness. These three hypotheses do not generate unique species-area formulae and the mathematical fit of any model does not signify the acceptance of a particular hypothesis (Connor and McCoy, 1979; May, 1975).

In a system of isolated areas of woodland each site is surrounded by other woods. These may act as potential sources of breeding colonisers or may maintain the number of species at a site by the continual immigration of non-breeding, vagile species. In the extreme latter case when the whole fauna is vagile, islands can be considered as different sized samples from a uniform species distribution, all the islands sharing the same species (Diamond and Mayr, 1976).

The total number of species and the number of vagile species, but not the number of poorly vagile species, was correlated with one measure of isolation, the area of woodland within 1 km of the site boundary. Only surrounding woodland has been considered as a source of immigrants to a site. Non-woodland scrub, permanent grassland and heathland may also support potential colonisers. For example 25 resident butterfly species have been recorded as breeding on roadside verges (Way, 1977).

For those vagile species which are not restricted to woodland (e.g. *Pieris brassicae, Aglais urticae*) woodland areas can be considered as samples from a uniform species distribution. The observed correlation between the number of vagile species and the area of woodland within 1 km of the site indicates that these species are subsidised by immigration from other areas.

Some species are restricted to woodland and are poorly vagile (e.g. *Ladoga camilla, Argynnis paphia*) and for these species woodland areas must be considered as true islands. The lack of correlation between the number of poorly vagile species and any of the measures of isolation, given in Table 1, does not demonstrate that isolation has no influence on the number of species because other parameters, apart from those given, may be important.

Connor and McCoy (1979) suggest that slopes of the regression of log S on log A within the range 0.20 to 0.40 are characteristic of the regression system whereas slope values deviating from this range may be of biological significance. High values have been attributed to highly interactive communities (Mason, 1978; Opler, 1974; Seifert, 1975) and to non-equilibrium land-bridge systems (Brown, 1971; Diamond and Mayr, 1976). The value of 0.50 in the present study is comparable to those found for other land-bridge and mainland systems. Bridges between sites, such as hedgerows and verges, may be important aids in the dispersal of the less mobile species (e.g. *Strymonidia w-album*) but are unlikely to be of importance in the movement of strong flying species (e.g. *Pieris brassicae*).

A maximum of 50% of the variation in the total number of species can be explained by variation in woodland area. Residual variation may be partly explained by historical factors, for woodland areas have unique management histories and contain unique communities. Major changes in woodland usage may eliminate certain larval food plants or butterfly species, e.g. *Aricia agestis* was eliminated from Assington Thicks when the wood was coniferised during the period 1957–71 (Data obtained from Biological Records Centre).

The present study shows that the number of butterfly species increases with woodland area. Single, large woods are more valuable for the maintenance of a high diversity of species than a number of smaller woods of an equivalent area in close proximity. The area of woodland required to support all the species recorded is 458 ha, estimated from the regression of the number of poorly vagile species against woodland area.

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