Distribution and abundance in British noctuid moths revisited

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The relationship between regional distribution and local abundance of British noctuid moths was studied using literature data. Distribution and abundance were strongly positively correlated at the scale of the UK, but at a smaller spatial scale no relationship was detected. Body size correlated negatively with abundance, while body size and regional distribution were weakly positively correlated. Food and habitat generalists were on average more abundant and more widely distributed than specialist species. Polyphages were larger in body size than oligophages/monophages. Regional distribution and potential population growth rate of the species were positively correlated. These results are in agreement with Brown's (1984) hypothesis that ecological generalists are both widely distributed and locally abundant.

1. Introduction

Andrewartha and Birch (1954) and Andrewartha (1961) defined ecology as the "scientific study of the distribution and abundance of organisms." Krebs (1978) proposed a practical version of Andrewartha's definition, and defined ecology as the "scientific study of the interactions that determine the distribution and abundance of organisms." Thus local abundance and geographical distribution of species are two key phenomena in population ecology, as the global population size of species is determined by these two variables (Ricklefs 1987). Lawton (1992) emphasized the importance of seeking general rules in population dynamics of living organisms; the relationship between distribution and abundance should reflect some such rules.

Several authors have demonstrated that abundance and distribution are usually positively correlated (e.g. Hanski 1982, Hanski et al. 1993, Bock & Ricklefs 1983, Bock 1984, Brown 1984, Gaston 1988 and Gaston & Lawton 1988a, b, 1990), but despite all efforts the causes of the positive relationship are still largely unclear. There are also some exceptions, i.e. abundant but local species, and widely distributed but scarce species. Such deviations from the general abun-

dance-distribution relationship can often be explained by the habitat requirements of the species (Gaston & Lawton 1990). Habitat specialists can be very abundant in their most favoured habitat, but they are absent elsewhere. There are not many generally scarce and widely distributed species.

Three hypotheses have been proposed to explain the positive relationship between regional or geographical distribution and local abundance:

First, as locally scarce species are more difficult to detect than locally abundant species, the number of localities at which a species is found must be an increasing function of the average abundance of the species. Thus, the positive relationship between distribution and abundance may be a sampling artefact (Wright 1991).

Second, species with a restricted distribution are often specialized to a certain habitat and/or particular food resource in the habitat. Widely distributed species are often generalists, inhabit a wide range of habitats and have a broad diet. Generalists are often assumed to be good dispersers (e.g. Ebenhard 1991). Based on these observations, Brown (1984) suggested that differences in species' ecological requirements explain the positive abundance-distribution relationship. According to Brown's hypothesis, generalists are both more widely distributed and more abundant than specialists.

A third mechanism which may yield the positive relationship between distribution and abundance is metapopulation dynamics (Hanski & Gilpin 1991, Hanski 1991). According to this hypothesis, high dispersal rate increases the number of occupied sites and hence distribution, and as there are more dispersers in abundant than scarce species, a positive relationship between distribution and abundance may emerge (Hanski & Zhang 1993, Hanski et al. 1993).

I examined these three hypotheses with data on British moths (Noctuidae). Gaston (1988) has previously studied the same assemblage of species in Britain. I use the same source of information on abundance (Rothampsted Insect Survey; Taylor & Woiwod 1980) but my distribution data are much more detailed (see below). I also studied the relationships between the distribution, abundance, body size, habitats, feeding specificity and fecundity of moths. Furthermore, I have studied the distribution-abundance relationship

at two spatial scales, at the scale of the whole of the UK (as Gaston 1988 did) and within ten 10000 km^2 squares in England and Wales. Finally, I have extended the analysis to all noctuid moths in the UK (abundance data from Woiwod & Taylor 1984, Taylor et al. 1985), whereas Gaston (1988) focused on the more abundant species for which more detailed information is available.

2. Material and methods

Most of the information about noctuid moths comes from Heath & Emmet's (1979 & 1983) monumental work on British moths and butterflies, which gives presence/absence data on the regional distribution of all moth species in the British Isles. I acquired a measure of the extent of moth distribution by manually counting the numbers of 100 km^2 squares in which moth species were recorded on Heath & Emmet's maps. I also computed the number of 10000 km^2 squares the species had been recorded in out of the total of 57, which gives another, cruder measure of distribution. I excluded from the latter measure a few 10000 km^2 squares, which lay mainly in the sea or an islands (Hebrides, Shetland, Orkney-islands, Channel-islands, Scilly-islands). Distribution data were available for 312 species.

A total of 174 noctuid species were available for the analysis. The abundance of 114 species in the British Isles is reported in the Rothamsted Insect Survey's results (Taylor & Woiwod 1980), and more recent papers give the abundance for 60 additional, rarer species (Woiwod & Taylor 1984, Taylor et al. 1985). Light-traps have been placed in a wide range of environments and they have been operated in the years 1967–82. A measure of abundance for each moth species is based on samples from a minimum of 32 sites and a maximum of 126 sites per year, located throughout Britain. The abundance measure used here is the log-transformed average per year abundance-when-present in the entire light-trap material. In addition, information about abundance of moth species was available for 10 individual localities which are situated in 6 different 10000 km^2 squares in England and Wales.

I collected data on several biological characteristics of the species, including body size, habitat, food plants and fecundity. A measure of body size was calculated as the arithmetic mean of the maximum and minimum adult wing-span in mm as given by Heath and Emmet. If different values were given for males and females, or for spring and summer generations, I used the mean for the sexes and the generations.

I formed six different habitat classes and placed each moth species in the class which it prefers in Britain. The habitat classes were: (1) deciduous woods and parks; (2) fields, grasslands, roadsides and gardens; (3) heath and moorland; (4) marine coasts; (5) marshes, wet meadows and common reed *Phragmites australis*-stands; and (6) mountains and hills (more than 250 m above sea level). The seventh class includes habitat generalists, which are commonly found in several of the former habitat classes.

I classified the species according to the number and relatedness of their food plants. These classes were: (1) larvae feed on one plant species (monophages); (2) on several plant species, which all belong to the same genus (oligophages sensu stricto); (3) on several plant genera, which all belong to one plant family (oligophages sensu lato); (4) on several plant families (polyphages); and (5) host plants unknown.

My second feeding type classification was based on life forms of the host plants: (1) larvae feed on grasses and twigs; (2) on bushes and trees; (3) on both bushes and trees, and on grasses and twigs; (4) on lichens and fungi; and (5) larval food plants unknown. I collected data about the potential population growth rate from a Bohemian source (Spitzer et al. 1984), as

British data are not available. I found data for 29 British species of moths, for which the potential population growth rate (PGR) is given by the formula,

$$PGR = Ng \ln (F/2), \qquad (1)$$

where F = the egg number per female and Ng = number of generations per year.

I used the SAS statistical software to analyse the data. Table 1 summarizes the distributions of the various variables studied. None of the quantitative variables was normally distributed. Neither logarithmic nor square-root transformations normalized the distributions. I therefore used nonparametric methods in most analyses.

There are several caveats to the interpretation of these results. Data on small-scale distribution, abundance, host plants and fecundity of moths are imperfect. Furthermore, data on abundance of rare moths (almost half of the species) are lacking. In contrast, the geographical distribution of these species in the UK is well known.

Light-trap sampling may be a selective method in estimating the abundance of moth species. Some species are more attracted to light than others, larger species usually fly higher and further than smaller ones, and response to light may not be similar in different habitats (Taylor & Woiwod 1980, Taylor et al. 1980 and Taylor & Woiwod 1982 discuss such problems with these data).

Host plants of many moths are still relatively poorly known. In addition, diet may vary substantially from one locality to another, and some moth larvae feed on different plants during their development (see Heath & Emmet 1979, 1983).

Table 1. Number of 100 and 10000 km² squares in which the species was recorded in Britain measure the distribution of the species, log density is the mean abundance-when-present of the species on a logarithmic scale in the Rothampsted data. Calculations of the wing-span and potential population growth rate (PGR) of the species are explained in the text. Number of observations (*N*), mean value , standard deviation (*SD*), coefficient of variation (*cv*), minimum value (*min*) and maximum value (*max*) for the variables.

Variable	*n*	mean±*SD*	*cv* (%)	*min*	*max*
100 km² squares	312	368.20±351.10	95.4	1.00	1559.00
10000 km²	312	29.70± 7.10	57.6	1.00	55.00
Log density	174	0.17± 0.76	455.5	−1.29	1.91
Wing-span (mm)	312	37.50± 8.20	21.9	17.00	85.00
PGR	29	6.54± 3.02	46.2	3.83	13.47

Therefore, a classification of moths according to their host plants is somewhat arbitrary.

Nonetheless, the data analysed in the paper represent the best insect data available.

3. Results

Sixty-three percent of the species were classified as habitat specialists occurring in only one of the six habitat classes and 37% as habitat generalists (Table 2). Among the habitat specialists there were 143 species occurring in deciduous woods, marshes and grassland, but only 52 species specializing in coasts, heaths and hills.

The number of polyphagous species was about the same as the number of oligophages/ monophages (Table 2). Twenty percent of the species were monophagous, with the common reed and oak *Quercus robur* being the most common larval food plants. The great majority of the species feed mainly on grasses and twigs, whereas about one fifth feed mainly on trees and bushes (Table 2).

The positive relationship between regional distribution and mean abundance is significant regardless of which measure of distribution is used (Figs. 1 and 2). There was no significant relationship between the number of 100 km² squares occupied in Britain and the body size of the moth, but as expected, smaller species tended to be more abundant than large ones (Fig. 3).

The number of 100 km² squares occupied in Britain was positively correlated with potential population growth rate for the 29 species for which the latter data were available (Fig. 4). Local population abundance and potential population growth rate were not correlated. The relationship between the two measures of distribution, occurrence in 100 km² squares and occurrence in 10000 km² squares, was curvilinear (Fig. 5), reflecting the faster approach to the maximum distribution at the cruder scale.

All the correlations between the number of 100 km² squares occupied, mean abundance and wing-span were statistically significant when the effect of the remaining variable was allowed. The positive correlation between abundance and

Table 2. Numbers and proportions (in brackets) of the total of 312 moth species in the various categories of habitat and food plant selection. Habitat preference: (1) deciduous wood, (2) grassland, (3) heath, (4) marine coast, (5) marsh, (6) hill, (7) generalist. Relatedness of larval food plants: (1) monophage, (2) oligophage (sensu stricto), (3) oligophage (sensu lato), (4) polyphage, (5) unknown. Lifeform of larval food plants: (1) grass/twig, (2) bush/tree, (3) grass/twig and bush/tree, (4) lichen/fungi, (5) unknown. For further explanation of the variables and the categories see material and methods.

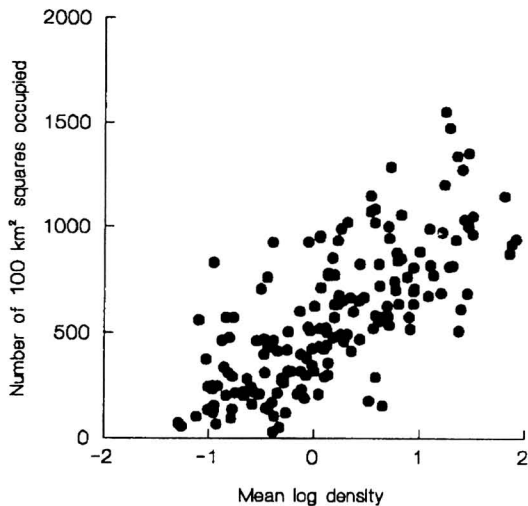| Habitat and food plant category	Habitat preference plants		Relatedness of larval food plants		Life form of larval food	
1	58	(18.6)	62	(19.9)	179	(57.4)
2	43	(13.8)	23	(7.4)	59	(18.9)
3	14	(4.5)	64	(20.5)	59	(18.9)
4	30	(9.5)	152	(48.7)	4	(1.3)
5	42	(13.5)	11	(3.5)	11	(3.5)
6	8	(2.6)				
7	117	(37.5)				
Total	312	(100.0)	312	(100.00)	312	(100.00)

Fig. 1. Relationship between distribution (number of 100 km² squares occupied) and abundance-when-present (mean log density averaged across sites) for 174 species of moths. rho = 0.747, *P*<0.0001.
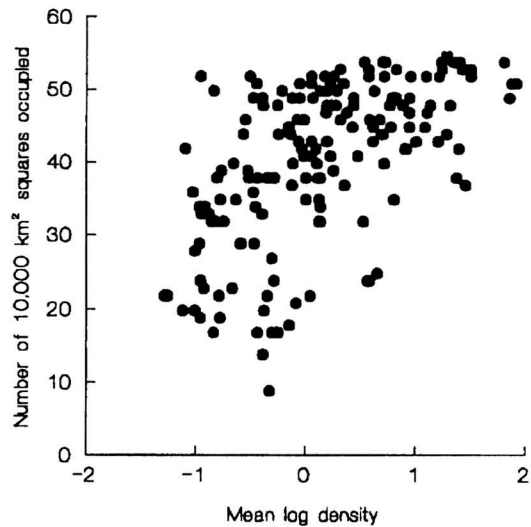

Fig. 2. Relationship between distribution (number of 10000 km² squares occupied) and abundance-when-present (mean log density averaged across sites) for 174 species of moths. rho = 0.617, *P*<0.0001.
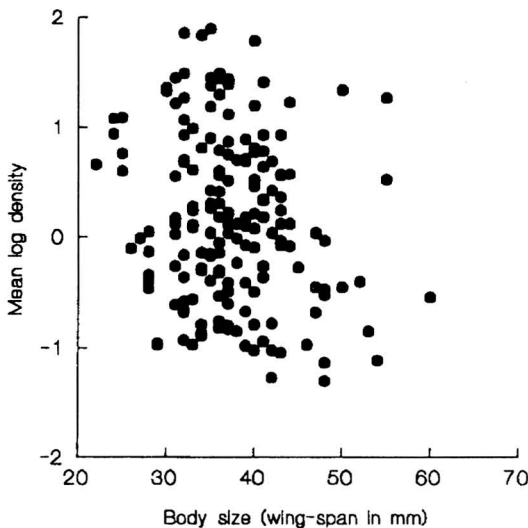

Fig. 3. Relationship between abundance-when-present (mean log density averaged across sites) and body size (wing-span in mm) for 174 species of moths. rho = – 0.159, *P*<0.05.
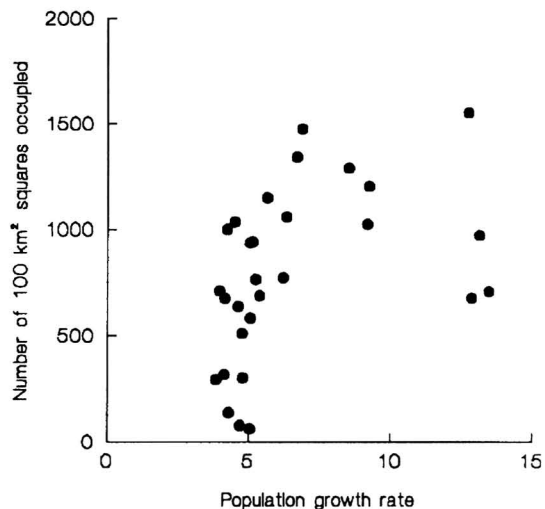

Fig. 4. Relationship between distribution (100 km² squares occupied in Britain) and potential population growth rate in Bohemia (Formula I) for 29 species of moths. rho = 0.582, *P* = 0. 0009.

distribution (body size effect allowed) was very strong (Spearman coefficient = 0.758, $P<0.0001$). The positive correlation (rho = 0.187, $P = 0.0136$) between body size and distribution (abundance effect allowed), and the negative correlation (rho = -0.244, $P = 0.0012$) between abundance and body size (distribution effect allowed) were weaker but significant.

I regressed mean abundance, body size and potential population growth rate against the number of occupied 100 km² squares. Multiple regression results indicate that body size and potential population growth rate affect regional distribution independent of the effect of abundance: large and high-fecundity moth species are most widely distributed (Table 3).

To study whether the positive relationship between distribution and abundance could be detected on a smaller spatial scale I calculated Spearman's correlation coefficients between abundance estimates for the species in ten 10000 km² squares in England and Wales and the number of occupied 100 km² squares within the corresponding 10000 km² squares. Only one of the ten correlations between distribution and abundance in the 10000 km² squares was statistically significant.

I studied the effect of habitat selection and food plant selection on regional distribution and local abundance with Kruskal–Wallis's nonparametric analysis of variance. Habitat selection was associated with the number of occupied 100 km² squares (Table 4). Habitat generalists had the widest occurrence (Table 5). Habitat selection was also associated with mean abundance (Table 4), with habitat generalists being the most abundant (Table 5).
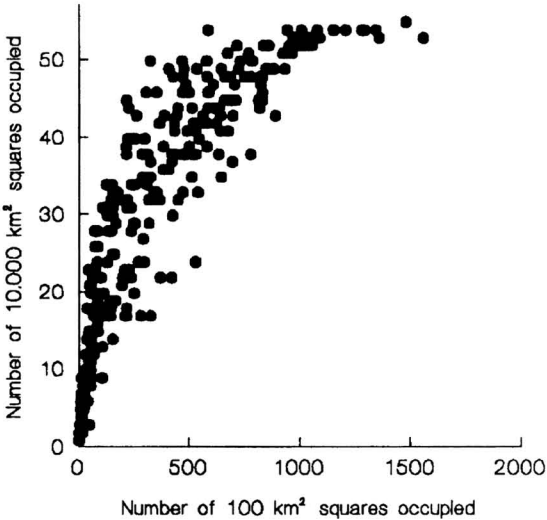

Fig. 5. Relationship between two measures of distribution for 312 species of British moths. rho = 0.946, P = 0.0001. Horizontal and vertical axes give the numbers of 10000 km² and 100 km² squares occupied, respectively.

Food plant selection was associated with regional distribution (Table 4): generalists occurred in a larger number of 100 km² squares than specialists (Table 5). Food plant selection was also associated with mean abundance (Table 4), though not very strongly. Generalist moths were most abundant (Table 5).

I finally studied the effect of body size on food plant selection with Mann-Whitney's U-tests. The 152 polyphagous species were larger on average than the 149 oligophagous/monophagous species (sum of Wilcoxon scores 20209.0, $Z = -3.0367$, $P = 0.0024$). The 59 moths that forage on bushes and trees were

Table 3. Multiple regression models of the regional distribution of noctuid moths. The dependent variable is the number of 100 km² squares occupied. The independent variables are abundance (average local abundance-when-present, logarithmic scale), body size (wing-span in mm) and potential population growth rate (PGR) (Formula 1).

Model	Independent variables	coeff.	t	P	R²
Model I	abundance	330.97	14.880	0.0001	(n = 174)
body size	9.30	3.494	0.0006	0.56	
Model II	abundance	351.58	6.579	0.0001	
(n = 27)	body size	17.99	2.793	0.0103	
	PGR	39.03	2.877	0.0085	0.73

slightly bigger than the 179 species foraging on grasses and twigs but the difference was not significant (sum of Wilcoxon scores 7654.5, $Z = 1.3176$, $P = 0.1876$).

4. Discussion

The positive relationship between local abundance and local/regional/geographical distribution of species has been previously demonstrated for a variety of taxa (Järvinen & Sammalisto 1976, Hanski 1982, Bock 1984, 1987, Bock & Ricklefs 1983, Brown 1984, Gaston 1988, Gaston & Lawton 1988a, b, Wright 1991 and Hanski et al. 1993). A negative correlation between abundance and distribution reported for Australian land birds is a notable exception (Schoener 1987, Ford 1990), and some studies have not detected a relationship between local abundance and regional/geographical distribution (e.g. Thomas & Mallorie 1985, Spitzer & Leps 1988).

Gaston & Lawton (1990) explained the observed deviations from the general positive relationship between distribution and abundance by habitat effects: a negative relationship may appear if abundance is measured from an unrepresentative habitat type. But when abundances are averages across several regionally representative habitats throughout the area over which distribution is measured, as in the British moth data, a positive relationship between distribution and abundance should appear. Like Gaston (1988), I found a positive relationship between local abundance and regional distribution in noctuid moths at the scale of the UK. However, on the scale of 10000 km²

Table 4. Kruskal-Wallis's nonparametric analysis of variance for 312 species of noctuid moths. The dependent variables are distribution (the number of 100 km² squares occupied) and local categorial variables are habitat selection, relatedness of larval food plants (Food1) and life form of larval food plants (Food2). For an explanation of the habitat and feeding categories see the text.

Categorial variable	Distribution H^2	df	P	Abundance H^2	df	P
Habitat	105.01	6	0.0001	16.24	5	0.0062
Food1	63.36	4	0.0001	10.46	4	0.0333
Food2	15.19	4	0.0043	8.88	4	0.0642

squares, this relationship did not emerge. This result may be due to an unrepresentative locality from which abundance data were obtained (only a single locality for each 10000 km² square), or possibly the small-scale distribution is underestimated, as suggested by Fig. 5.

Habitat selection of the moth species is clearly associated with their regional distribution, habitat generalists and polyphages having on average the widest regional distribution and specialists having the most restricted distribution. Bock & Ricklefs (1983), Thomas & Mallorie (1985) and Kouki & Häyrinen (1991) have, among others, demonstrated that habitat specialists are not usually so widely distributed as habitat generalists.

My results support Brown's (1984) hypothesis about the distribution-abundance relationship, because in addition to their wider regional distribution, polyphagous moths and habitat generalists also had a higher average local abundance than oligophagous/monophagous species and habitat specialists. Brown suggested that trophic generalists will usually be more abundant than specialists, because of the greater sum of resources which they can exploit: McNaughton & Wolf (1970) and Hanski & Koskela (1978), among others, have found a

Table 5. The mean scores in the various categories of habitat and food plant selection in the analysis in Table 4. The categories are explained in Table 2 = missing data.

Category		Distribution	(n)	Abundance	(n)
Habitat	1	151.2	(58)	81.6	(36)
	2	150.1	(43)	90.7	(21)
	3	122.5	(14)	29.8	(8)
	4	63.3	(30)	76.0	(3)
	5	113.0	(42)	71.0	(15)
	6	35.4	(8)		
	7	213.3	(117)	97.2	(91)
Food1	1	87.9	(62)	74.5	(15)
	2	122.3	(23)	66.5	(11)
	3	171.2	(64)	76.3	(35)
	4	187.6	(152)	95.9	(111)
	5	99.0	(11)	28.8	(2)
Food2	1	147.6	(179)	88.2	(91)
	2	159.7	(59)	74.2	(34)
	3	191.5	(59)	100.7	(44)
	4	149.5	(4)	62.7	(3)
	5	99.0	(11)	28.8	(2)

positive relationship between niche breadth and local abundance. On a small spatial scale, as, for example, on a single host plant, specialists are usually more abundant than generalists (e.g. Gaston & Lawton 1988b, Readfearn & Pimm 1988). However, scarce species are often (e.g. Bock & Ricklefs 1983, Thomas & Mallorie 1985, Väisänen & Rassi 1990) but not always (e.g. Kouki & Häyrinen 1991) habitat and/or food specialists.

Metapopulation models, too, predict a positive relationship between distribution and abundance (Hanski 1991). According to the metapopulation hypothesis, local abundance should decrease but distribution should increase with emigration rate (Hanski & Zhang 1993). Assuming that in moths migration rate increases with body size, the present results are in agreement with this prediction. The positive relationship between body size and regional distribution is also significant in Gaston's (1988) analysis of British moths. On the contrary, Gaston & Lawton (1988a, b) found a negative correlation between body size and regional distribution in bracken insects. The relationship between body size and migration rate probably depends on whether migration is active (as in most moths) or passive (probably in many small insects, incuding many bracken herbivores).

Gaston (1988) did not find a significant negative relationship between local abundance and body size as I did. The positive relationship between regional distribution and body size is weak in both analyses. My multiple regression analysis confirmed that body size contributes to regional distribution independently of the effect of abundance. Gaston (1988) found feeding specificity not to be associated with local abundance, but in my more extensive data generalist moths were more abundant than specialist species. I also found support for the notion that larger moths and butterflies tend to be more polyphagous than small species (e.g. Wasserman & Mitter 1978, Niemelä et al. 1981, Brown & Maurer 1986, Gaston 1988).

5. Conclusions

My results confirm the strong positive relationship between regional distribution and average local abundance in British noctuid moths. These results support Brown's hypothesis that ecological generalists are both more widely distributed and locally more abundant than specialists. Hanski and Zhang's metapopulation hypothesis is consistent with the present results, on the assumption that migration rate and body size are positively correlated in noctuid moths. The metapopulation and ecological specialization hypotheses may not be entirely independent, as the probable superior dispersal ability of generalist species which tend to be large establishes a link between Brown's (1984) and Hanski & Zhang's (1993) theories.

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