Habitat island or habitat mosaic?

A case study of heathlands in southern England

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1. Introduction

Heathland is a community dominated by ericaceous dwarf-shrubs. There are extensive areas of this community in several parts of north-western Europe; in northern France, Belgium, the Netherlands, north Germany, Denmark and southern Sweden, and in Great Britain. The community is dominated by *Calluna vulgaris* growing in association with 5 or 6 other species. One of the characteristics of heathland is that it is a species poor community. This type of vegetation, which grows on poor siliceous soils (mineral soils), differs slightly from similar communities growing at higher altitudes (250 m) in organic (peat) soils; this latter community is often called moorland, and although there is an arbitary difference between the two, in floristic terms they represent a continuim.
Heathland vegetations spread in almost all areas following late Neolithic forest clearances about 3000–4000 years ago. Beneath most heathlands there are well developed humus-iron podsols and the rate of podsolisatiom may have increased through the removal of the forests. In Dorset, as in most of southern Britain, heathland vegetation was well established by Roman Times (about 2000 years ago) (WEBB & HASKINS 1980). The open landscape was maintained by a combination of activities, which included grazing by cattle, sheep and ponies, turf and peat cutting, and the gathering of *Ulex* for fuel and of *Pteridium* for animal bedding, and the periodic burning of the vegetation. All of these activities prevented the regeneration of the woodland. The role of fire is questionable, since grazing and turf cutting alone would have been sufficient to maintain heathland vegetation as it was in the Netherlands and in north Germany (GIMINGHAM & De SMIDT 1983). Fire may have been introduced in the eighteenth century following its introduction to the uplands to manage sheep and grouse moors (GIMINGHAM 1972). Today in southern Britain, almost all of the heathland is maintained by periodic burning, which is often accidental and extensive, rather than controlled and on rotation. Rotational management also assumes that the effects of area and isolation are not such as to curtaine its success, and that local extinctions of species are to be expected.
It is important to recognize that these heathlands are plagio-climax communities and that man has influenced them for several millennia, and, that without his continued interventation, there would have been secondary succession to forest (GIMINGHAM, CHAPMAN & WEBB 1979). This evidently happened in the past since pollen diagrams show increases in the proportions of scrub species such as *Corylus* (WEBB & HASKINS 1980). For nature conservation

Tabelle 1

Estimates of the area of heathland in Dorset (from WEBB & HASKINS 1980)

1750	39960 ha
1811/1817	30400 ha
1896	22672 ha
1931/1934	18200 ha
1960	10000 ha
1973	6100 ha
1978	5832 ha

purposes it is important to recognize that succession must be arrested.
From Roman Times until the mid-eighteenth century, it is thought that the extent of the heathland in Dorset changed little, but after this time improvements in agricultural methods enabled much of the heathland to be reclaimed (WEBB & HASKINS 1980). In 1759, it was estimated that there were about 40000 ha of heathland on soils formed Tertiary deposits in south-east Dorset. These heathlands were on ten large blocks separated by rivers. Various estimates have been made of the area of heathland at dif-

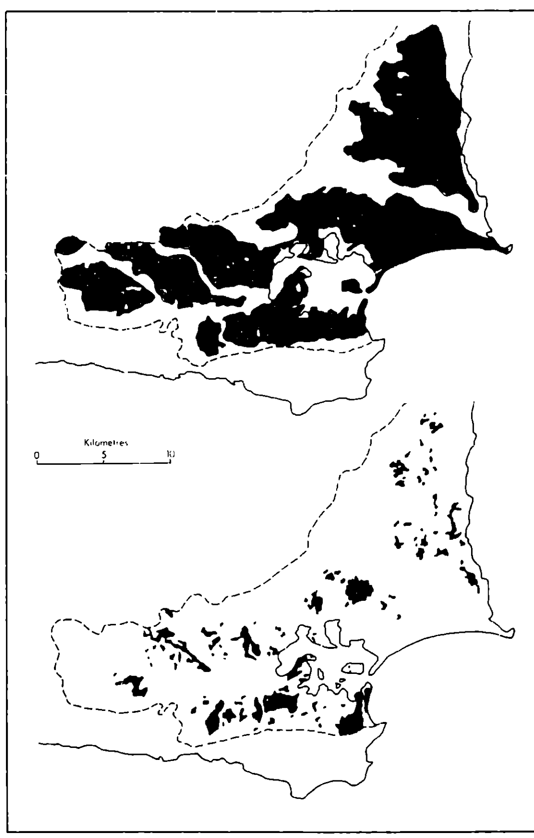

Abbildung 1

The decrease in area and the increase in fragmentation of heathland in south-east Dorset (part of southern England) between 1759 und 1978 (from WEBB & HASKINS 1980).

ferent times since then (Table 1). These are cartographic estimates and much be considered to represent heathland in its widest definition. A field survey was made in 1960 (MOORE 1962) which estimated there to be 10000 ha of heathland remaining. Moore also used a wide definition of heathland which he considered to be the »whole inter-related complex of plant communities associated with poor soils«. This definition included areas dominated by *Calluna vulgaris* and *Erica* spp., valley mires, pine heath, *Ulex* scrub and acid grasslands dominated by *Agrostis curtisii* or *Molinia caerulea*. In contrast, WEBB & HASKINS (1980) mapped only the areas of ericaceous dwarf-shrubs and valley mires. Using this narrower definition of heathland, WEBB & HASKINS (1980) estimated the area of heathlands to be 5832 ha, but had a wider definition, similar to that of MOORE (1962), been adopted it is likely that the area would have been about 7000 ha.
The main losses of the heathlands have been due to, reclamation for agriculture, afforestation, and industrial and urban development.
Not only has the area of these heathlands been greatly reduced, but there has been considerable fragmentation (Figure 1), a process analogous to continental drift. WEBB & HASKINS (1980) estimated there to be 768 fragments (Table 2) of which 476 (62 %) were less than 1 ha and only 14 larger than 100 ha. WEBB & HASKINS (1980) used a stringent definition of isolation, but it is almost impossible to divise a definition which is biologically meaningful, and it likely that separate definitions are needed for individual species.
The heathlands of Dorset have a high priority for nature conservation, since this is an area of Britain which showns transitions in the distribution of continental and oceanic species. For these reasons, and because there is still a continuing loss of heathland, a programme of research was initiated to assess the biological consequences of fragmentation and isolation, particularly on the invertebrate communities.

2. Sampling Sites

The planning of a sampling programme was influenced by ideas of island ecology and, in particular, the equilibrium model of MacARTHUR & WILSON (1967). Accordingly, twenty two heathlands which varied from 0,1 ha to 476 ha were chosen for sampling. The edges of the three largest heathlands were also sampled. The sampling sites were chosen to represent a range of differening degrees of isolation and were comparable in topography, age and structure of the vegetation. At each site, a sampling point was established as centrally as possible. The vegetation of the sampling sites was mature, dry heathland dominated by *Calluna vulgaris* growing in association with *Erica cinerea, Erica tetralix, Ulex minor* or *Ulex gallii* and often with scattered *Pteridium aquilinum*. The grasses present were with *Agrostis curtisii* or *Molinia caerulea*. The vegetation was recorded at each sampling location in two ways; first, the number of species and the mean height of the vegetation were recorded from within the area in which the pitfall traps were laid. Second, the percentage cover of each species was recorded in a 1 m^2 quadrat placed at each trap location, bare ground was recorded in a similar way and treated as a species.
At each sampling point ten pitfall traps were laid in the same configuration on every heathland; thus, the same sampling effort was made on every heathland irrespective of its overall area. It is important to appreciate that the fauna of the heathlands was sampled and not censused. Many studies of species-area relationships have been confined to vertebrates, especially birds, and higher plants, and it is possible for these species to census or record the presence of every individual of every species on an area. For invertebrates, this is impractable and samples must be taken. Hence the results presented in this paper are from samples which represent point or within habitat diversity or alpha diversity *sensu* WHITTAKER (1975). The crucial

Tabelle 2
The numbers of sites classified according to area within the heathlands of the Poole Basin (from WEBB & HASKINS 1980).

Area of site (ha)	No. of sites	% of total sites	Area (ha)	% of total area
0.1	159	21	5.38	0.1
0.1–0.9	317	41	108.35	1.9
1.9	204	27	653.67	11.2
10.19	32	4	409.88	7.0
20.29	19	3	454.67	7.8
30.39	5	0.7	182.36	3.1
40.49	5	0.7	228.56	3.9
50.59	3	0.4	174.26	3.0
60–69	3	0.4	198.36	3.4
70–79	5	0.7	377.89	6.5
80–89	1	0.1	83.24	1.4
90–99	1	0.1	93.57	1.6
100	14	1.8	2862.76	49.1
Total	768	—	5832.95	—

Tabelle 3

The correlations between variables, representing plant diversity on heathlands in the Poole Basin, and heathland area and total area of surrounding heathland (from WEBB & HOPKINS 1984).

	Log Area	Log Area 2 km
% Total Cover	0.29	0.20
S. D. Total Cover	-0.14	0.03
Height	0.28	0.14
S. D. Height	0.15	-0.25
Number of plant spp.	-0.54**	-0.50*
% Ericaceae	0.46*	0.39
% Ulex spp.	0.21	-0.36
% Gramineae	0.08	-0.09
% Bare Ground	0.15	0.28

Significance levels indicated by *0.05 >P>0.01, **P<0.01.

point is how point diversity is related to the overall diversity of the site. There is no reason to expect that the richness of species at a point (alpha diversity) to increase as the whole area of the heathland increases, although were the equilibrium theory of MacARTHUR & WILSON (1967) applicable, this would be the case (WEBB & HOPKINS 1984).
The area of each heathland was taken from the survey of WEBB & HASKINS (1980) and isolation was calculated by estimating the area of heathland within a 2 km radius of the sampling point.

3. Plant Diversity

A negative correlation was found between the richness of plant species and both the area of the heathland and the total area of surrounding heathland (a measure of isolation) (Table 3). The vegatation at the edges of the large heathlands contained more species than that at the centre. The cover of *Calluna vulgaris, Erica cinerea* and *E. tetralix (called % Ericaceae)* was partially correlated with the area of the heathlands and with the area of surrounding heathland (Table 3). This suggests that there is a decrease in the dominance of ericaceous dwarf-shrubs on the smaller heathlands and, that related to this, there may be a change in the structural diversity of the vegetation. Since heathland is characterised by a low plant species diversity, an increasing value for richness or diversity suggests a trend of deteriorating heathland quality (WEBB & HOPKINS 1984).

4. Invertebrate Diversity

The different groups of invertebrate animals showed a variety of trends (Table 4). In general, there was a negative correlation between the point diversity of invertebrates and heathland site area, and also between the total area of heathland vegetation within a 2 km radius (Figure 2). These relationships, significant at various levels, held for all species of Coleoptera (Total Coleoptera), a set of phytophagous Coleoptera (Phytophagous Coleoptera) and heathland Heteroptera. No significant correlation was obtained for all species of Araneae (Total Araneae), but a set of heathland Araneae a weakly positive but not significant correlation was obtained. Thus suggesting that on large heathlands the point diversity of those spiders (Araneae) dependant on heathland was greater on large heathlands than on small. This feature was investigated in more detail and the relative importance of heathland spiders in the community was investigated by defining an index (R);

$$R = 2 \sum^{S_H} R_i / S_T(S_T + 1)$$

where S_H is the number of heathland spider species, R_i is their rank in the rank abundance curve for the whole community, S_T is the total number of species of spider recorded. The index R was positively correlated with the areas of the heathlands (r = 0,50, P 0,05), which suggested that on large heathlands those species of spider dependant on heathland formed a larger proportion of the total spider community than on small heathlands.

Tabelle 4

Correlations between invertebrate diversity and site area and the area of heathland within 2 kms for heathlands in Dorset (from WEBB & HOPKINS 1984).

	No. of Species	Site Area (ha)	Area of Heathland within 2 kms
Total Coleoptera	272	-0.41*	-0.58**
Phytophagous Coleptera	65	-0.59**	-0.70***
Total Araneae	158	-0.07	-0.26
Heathland Araneae	60	0.38*	0.24
Heathland Heteroptera	15	-0.27	-0.46*

Significane levels: *0.05>P>0.01, **P<0.01, ***P<0.001

Tabelle 5

Equations summarising the results of multiple regression analyses between plant diversity and invertebrate diversity on the Dorset heathlands (from WEBB & HOPKINS 1984).

Total Beetles	
$S = 8.23\,(\ln T)^{*} + 0.56\,(Ulex) + 0.99\,(S.D.\ height)^{*} - 13.79$	$(r^2 = 0.65)$
Q = no significant regression	
Phytophagous Beetles	
$S = 1.96\,(\ln T)^{*} + 0.26\,(Ulex)^{***} + 0.04$	$(r^2 = 0.61)$
$Q = 0.09\,(Ulex)^{*} + 3.21$	$(r^2 = 0.12)$
Total Spiders	
$S = 10.52\,(\ln T)^{**} - 14.0$	$(r^2 = 0.31)$
$Q = 0.21\,(height)^{**} - 0.08\,(total\ cover)^{*} + 15.55$	$(r^2 = 0.36)$
Heathland Spiders	
$S = 5.60\,(\ln T)^{***} - 7.85$	$(r^2 = 0.60)$
$Q = 0.09\,(height)^{***} + 0.14\,(bare\ ground)^{**} + 0.85$	$(r^2 = 0.49)$

5. Compositional Differences

The catches of Coleoptera and Araneae were further examined by ordination techniques to identify patterns of variation in composition which may have been related to the areas of the heathlands or to their degree of isolation and to the composition of their vegetation (HOPKINS & WEBB 1984).

The ordination of the vegetation alone revealed local differences which could be related to the distribution of the two dwarf species of *Ulex, Ulex minor* and *Ulex gallii,* and to the distribution of *Erica tetralix,* and hence to possible variations in soil moisture content.

The ordination for Total Beetles was inconclusive and suggested that any variation in the composition of the beetle fauna of these heathlands could not be reduced to a few dimensions. An examination of the rank order of species with the highest component loadings suggested that for the set Total Coleoptera, large heathlands were characterised by a lack of species and not by the presence of particular species; again this suggested that edge effects may be important.

The set Heathland Araneae were the most interesting and the results of the ordination suggested that the first axis of variation was related to the quality of the vegetation as a habitat for spiders, which in turn was positively correlated with heathland area. Hence, large heathlands provided a better habitat for the heathland spiders than small heathlands.

Spiders disperse passively by drifting on threads of web and it seems possible that those species found on large heathlands, but absent or poorly represented on small ones were poor dispersers. This view was confirmed from an analysis of the captures of spiders by water traps. Those species found on both large and small heathlands were those with the greatest power of dispersal. The species with the poorest powers of dispersal were present on only the largest heathlands, and, furthermore, there were no species of heathland spider which occured on small heathlands which did not occur on large ones. These results indicate that, where a suitable set of species can be recognized, the general principles of island ecology can be applied, but the most difficult problem is to define suitable sets of species.

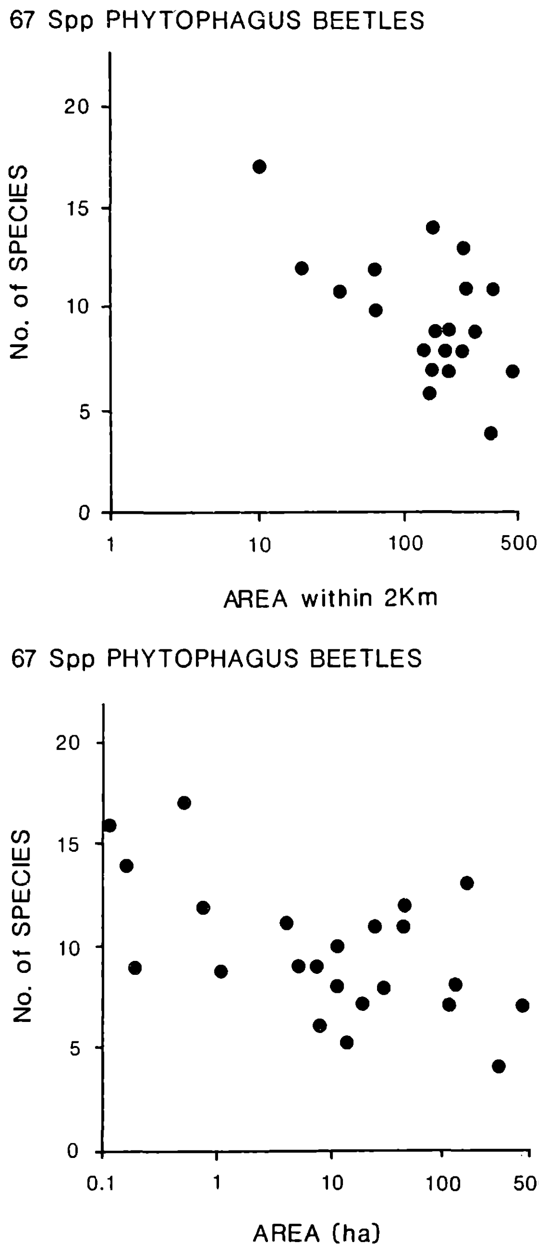

Abbildung 2

An example of the relationship found between the number of species and both the areas of the heathland patches and the total area of heathland in their surroundings (a measure of isolation).
This example is for phytophagous species of the Coleoptera.

6. Effects of Surrounding Vegetation Types

The regressors for heathland area and for the area of surrounding heathland were poor predictors of invertebrate diversity and, likewise, no single set of habitat features could be identified which accounted for a large proportion of the total variability in the composition of the fauna of these heathlands. WEBB & HOPKINS (1984) suggested, that in the case of species richness, edge effects may have been important in generating the observed diversities, and, that if this were the case, samples from small heathlands are likely to capture more vagrant species than those from large heathlands. In this case, area is a crude way of predicting edge effects, and since the same sampling effort was made on all sites, the captures, in part, record the distance from the edge at which the pitfall traps were placed. It seems likely that the composition and structure of the surrounding vegetation are important influences on the diversity and composition of invertebrates on the heathlands.
The relative proportions of eight surrounding vegetation types, obtained from the survey of WEBB & HASKINS (1980), were used as variables representing vegetation composition in step-wise multiple regression analysis (WEBB et al. 1984). The correlations obtained between these eight vegetation types for four sets of invertebrates is given in Table 6. For the set Total Coleoptera the area of heathland within a 2 km radius of the sampling point was the only significant regressor; R^2 = 42 %, where S = 55,24 – 2,40 $\log_{10}$ (heathland within 2 kms) – 0,12 (% grassland) – 0,15 (% of bare ground).
R^2 is the percentage of the variation its species richness (S) explained by the equation.
For the set Phytophageous Coleoptera, besides the effect of the total area of heathland within a 2 km radius, there was a partial correlation with the proportion of grassland surrounding each heathland (R^2 = 58 %), S = 18,70 – 4,63 $\log_{10}$ (heathland within 2 kms) + 0,04 (% grassland).
For the set Total Araneae, there was a weak positive correlation between species richness and the proportion of woodland surrounding a heathland and a significant negative correlation with the proportion of grassland, which was combined with a negative, but not significant, correlation with bare ground (R^2 = 49 %), S = 55,24 – 2,40 $\log_{10}$ (heathland within 2 kms) – 0,12 (% grassland) – 0,15 (% bare ground). These partial correlations suggested that there was a downward trend in the richness of spiders from woodland, through scrub and heathland to grassland and bare ground, reflecting changes in the structural diversity of these habitats. For the set Heathland Spiders there was no significant simple or partial correlations. It was interesting that the diversity of heathland spiders was unaffected by the presence of surrounding grasslands, and, that, unlike woodland spiders, grasslands species do not penetrate heathland.
The interpretation of the effects of surrounding vegetation is difficult, but, in general, it seems that where more structurally diverse communities sourround patches of heathland significant positive correlations can be found between the type of vegetations and the diversity of invertebrates. The likely effects of the different vegetation types surrounding a heathland are summarised in Figure 3. Where structurally more diverse communities surround the heathland there is a tendancy for diversity to increase and the composition of the fanuna to change. Less structurally diverse communities may result is a small loss of species from the heathland, the ideal solution is for there to be an appreciable area of other heathland in the vacinity of the area in which you are interested. Woodland, both deciduous and coniferous, and aquatic communities surrounding a heathland result in the greatest increase in diversity. Smaller increases result from the presence of carr and scrub. Only with various forms of grassland is there no increase in diversity. Because heathland is a species poor community these effects are more noticeable than in the case where a rich habitat is surrounded by poorer ones. However, even in this case there will be interactions with the surroundings (see for instance MADER 1981).

Tabelle 6

Correlations between the richness of species of Coleoptera and Araneae and variables representing the proportion of different vegetation types surrounding heathlands in Dorset (from WEBB et al 1984).

	Coleoptera	Phytophagous Coleoptera	Araneae	Heathland Araneae
Site area (ha)	−0.488*	−0.585**	−0.064	0.379
Area heathland 2 km	−0.583	−0.697***	−0.253	0.240
Marsh	−0.021	−0.201	0.238	0.142
Carr	−0.305	−0.106	−0.226	0.269
Scrub	−0.149	−0.196	0.131	0.127
Hedge	−0.271	−0.283	−0.316	−0.007
Woodland	0.422*	0.065	0.360	−0.142
Grassland	−0.232	0.317	−0.522*	−0.135
Bare Ground	−0.184	−0.282	−0.287	0.306
Open water	0.040	−0.057	0.415*	−0.037

10 % r = 0.360, 5 % r = 0.413, (*), 1 % r = 0.526 (**), 0.1 % r = 0.597 (***).

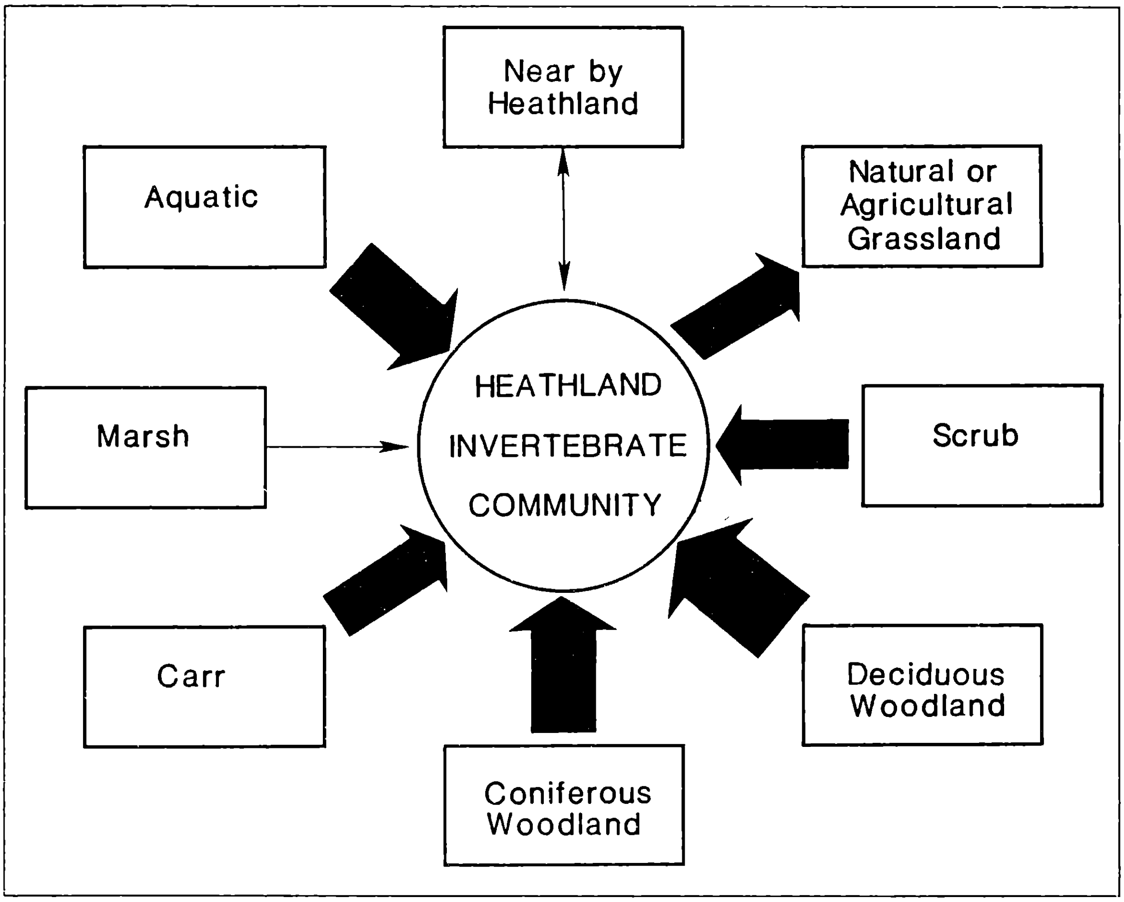

Abbildung 3

A diagram summarising the interactions between a patch of heathland and various types of surrounding vegetation. The results have been calculated from data obtained on invertebrates. The arrows indicate the direction of the effects and the width of the arrow is an estimate of the magnitude of the effects.

7. Discussion

There is evidently an interaction between heathland patches and their surroundings. This is made apparent because heathland is a species poor community, but such a feature is probably also to be found in other communities, although its effects may be masked. Clearly, to minimise edge effects patches of heathland chosen as nature reserves should be as large as possible, but we do not yet have evidence for the size required, although it is thought to exceed 10 ha. As an alternative, a cluster of smaller areas might be acceptable. Small isolated patches of heathland are probably not viable in the long term and will be difficult to maintain because of edge effects. Heathland is a seral community and management must be undertaken regularly to arrest succession, this in unlikely to be possible on small sites and therefore larger reserves are needed. In fact, small heathlands surrounded by othe communities may not really be heathland in the accepted sense of the term, they may be no more than part of the heterogenity of the communities surrounding them.
WEBB & HOPKINS (1984) have pointed out that high levels of invertebrate diversity are indicative of deterioration heathland conditions, and that diversity alone is not an adequate criterion for either choosing nature reserves or for assessing the effects of management. The species composition of the community is also important. Since edge effect are one of the main factors contributing to high levels of diversity, it might be important to choose reserves with vegetation types surrounding them which are complementary. This creates something of a paradox conservationists, since reserves tend to be chosen for their high diversity. If a combination of areas, adjecent to heathland, are chosen for their high diversity this will impair the perpetuation of the heathland.
Related to these problems ist the general one of whether species or community conservation is being practised. When rare species occur on small sites these sites will undoubtably need conserving, but elsewhere the emphasis may be on the community, and hence species composition is as important as diversity. We are thus faced with what is an appropriate model for patches or islands of habitats in surroundings representing many different communities. Should be regard the habitat in which we are interested as an island or should be consider it to be part of a mosaic? The MacARTHUR & WILSON equilibrium model can be applied in certain circumstances to habitat islands, but since there appears to be a considerable interaction between these islands and their surroundings it may not be appropriate. A weakness of the MacARTHUR & WILSON model is that it deals explicitly with the numbers on species only and not

with the development of community structure (WILLIAMSON 1981). Therefore if the structure and composition of the community on a given area is likely to be affected by species from the surrounding communities the MacARTHUR & WILSON model may not be the most appropriate one for a patch-work of habitat islands. Such islands are not isolated from one another in the same way as oceanic islands, and it is possible for colonists to survive in the surroundings. The present work on the Dorset heathlands suggests that there is considerable interaction between patches and therefore a model which recognizes this mosaic type of structure, (as for instance in the Pine Barrens of New Jersey, FORMAN 1979), and the extent to which they interact seems more appropriate.

8. Acknowledgements

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9. Zusammenfassung

Die Heideflächen in Süd-Ost-Dorset wurden 1759 auf 40000 ha Fläche geschätzt; 1960 waren davon noch ca. 10000 ha und 1980 5832 ha vorhanden. Die Flächen wurden in landwirtschaftliche und forstwirtschaftliche Flächen sowie in Industrie- oder Siedlungsflächen umgewandelt.
In einem Forschungsprogramm wurden die biologischen Konsequenzen von Isolation und Zersplitterung am Beispiel von 20 unterschiedlich großen (0,1 ha bis 476 ha) Restflächen untersucht.
Zwischen Pflanzenvielfalt und Untersuchungsfläche ebenso wie zwischen Pflanzenvielfalt und Isolationsgrad wurde eine negative Korrelation beobachtet.
Auch für phytophage Käfer stellte sich eine negative Korrelation zwischen Untersuchungsfläche und Artenvielfalt sowie zwischen Isolation und Artenvielfalt heraus. Bei Spinnen war dagegen eine schwach positive Korrelation festzustellen. Dieses abweichende Resultat hängt möglicherweise mit den Verbreitungsmechanismen der Spinnen zusammen.
Für die Artenzusammensetzung und die Anzahl der vorgefundenen Arten in den Untersuchungsflächen scheinen Randeffekte von großer Bedeutung zu sein.
Bei der gewählten Untersuchungsmethodik – gleiche Fallenzahlen im Mittelpunkt der Inselhabitate – ist mit einem wachsenden Einfluß der Randzonen und der sie besiedelnden Arten mit abnehmender Flächengröße zu rechnen.
Für die Spinnenfauna zeigte sich, daß große Heideflächen bessere Habitate darsteilen als kleine Flächen.
Es wird gezeigt, daß die Zusammensetzung und Struktur der umgebenden Vegetation die Vielfalt und Artenzusammensetzung der Wirbellosen in Heideflächen maßgeblich beeinflussen. Werden Heideflächen von strukturreichen Pflanzengesellschaften umschlossen, steigt die Artenvielfalt, und die Artenkomposition wandelt sich. Diese Effekte werden besonders bei angrenzenden Waldflächen und Feuchtgebieten deutlich.

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