



British Ecological Society

Competition and the Structure of Ecological Communities

Author(s): Charles Elton

Source: *Journal of Animal Ecology*, Vol. 15, No. 1 (May, 1946), pp. 54-68

Published by: [British Ecological Society](#)

Stable URL: <http://www.jstor.org/stable/1625>

Accessed: 07/01/2011 12:17

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=briteco>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



British Ecological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Animal Ecology*.

<http://www.jstor.org>

COMPETITION AND THE STRUCTURE OF ECOLOGICAL COMMUNITIES

BY CHARLES ELTON, *Bureau of Animal Population, Oxford University*

(With 1 Figure in the Text)

1. AN ANALYSIS OF SOME COMMUNITY SURVEYS

(a) *General*

If one peruses the lists of species recorded in various ecological surveys of clearly defined habitats, the thing that stands out is the high percentage of genera with only one species present. This is quite a different picture from a faunal list for a whole region or country, in which many large genera are to be found.

There are, of course, theoretical difficulties in deciding exactly what we mean by a clearly defined community or a major habitat, and also considerable practical difficulties during ecological survey work in the field in separating genuine inhabitants from accidental visitors, especially as some of the latter may play a real part in the life of the community. The following analysis is made with clear realization that all community surveys to a certain degree set arbitrary limits to the radiating connexions between species. Such partly arbitrary sections of the larger system of interspersed habitats with their communities will nevertheless show something of the typical structure, without supplying a complete story.

(b) *Animal communities*

Table 1 gives analyses of fifty-five ecological surveys of animal communities from an extremely wide range of habitats. In three instances some grouping has been adopted to give more reliable figures, which reduces the total to forty-nine units, distributed among twenty-one major types of habitat. The communities cover land, fresh-water, estuary and marine; Arctic, Subarctic, Temperate and one Tropical; free-living and parasitic; and mostly include a very large proportion of the groups of animals present in each habitat.

The percentage of genera with only one species present varies from 69 to 100%, but the greatest frequency is centred round 85%, while about three-quarters of the figures lie between 81 and 95% (Table 2). The corresponding percentage of the number of species belonging to genera in which only one species is present varies more widely, from 46 to 100%. The greatest frequency lies between 71 and

85%, and about three-quarters of the figures lie between 66 and 90% (Table 3).

Genera with four or more species present form a very small fraction of the whole—on the total figures, only 1.32%. In the fifty-five communities, only eleven recorded five or more species in the same genus; while there is only one instance of more than six (in no. 22). These facts are expressed in the figures for the average number of species per genus in each community, which in all instances lies between 1 and 2, the average for the whole lot being 1.38 (range 1.00–1.63). This is shown in another way in Fig. 1, which indicates something like a straight-line relationship between the number of species and number of genera in an animal community.

It is necessary to discuss the validity of the survey data a little, before considering the explanation of these relationships between genera and species:

(1) The range of habitats included is very wide, but it does not contain samples of the most complex habitats, particularly woodland, for the reason that no complete ecological surveys of them have yet been done. Such communities might prove to differ in their structure from those of the simpler kind. This point is discussed again in § 2(b).

(2) There is really no such thing as a uniform habitat, since all habitats consist of interspersed mosaics of micro-habitats or are internally patchy in the distribution of population densities (as with plankton); and since they also are subject to variations in conditions caused by seasonal and other temporal changes. The habitat units chosen as samples have fairly uniform habitat patterns within them, and provide well-established ecosystems that have been studied fairly or very thoroughly by the surveyors.

(3) Few ecological surveys can be complete, yet many of those analysed are undoubtedly very nearly complete within the limitations of the collecting and recording methods used. These limitations usually affect whole groups of organisms, rather than genera within the same family or order, and so do not harm the present analysis. Thus a plankton net will collect all planktonic Crustacea but not any fish; the bottom sampling of benthos may ignore the micro-fauna; the log communities only give the invertebrates, not the

Table 1. Analysis of genus/species relations in fifty-five animal communities

General habitat	Community	No. of genera with the following nos. of species present						Total species analysed (B)	Total no. of genera analysed (C)	Average no. of species per genus (B/C)	% of genera with one species present (A/C)	% of 'single species' present (A/B)	Reference
		1 (A)	2	3	4	5	6						
Arctic fjeldmark	1a Frost-weathered rocky soil, Island	24	2	1	—	—	—	31	27	—	—	—	Summerhayes & Elton, 1923, pp. 221-2, 245, 262-3
	1b Rocky Lowland, Prince Charles Foreland, Spitsbergen	13	1	—	—	—	—	15	14	—	—	—	
	1c Raised beaches, Kilaas Billen Bay, West Spitsbergen	14	8	1	—	—	—	33	23	—	—	—	
	1d Lowland, Reindeer Peninsula, West Spitsbergen	17	5	2	1	1	—	42	26	—	—	—	
Subarctic fjeldmark	1a-d Average	17	4	1	0.25	0.25	—	30.25	22.5	1.35	75	56	Davis, 1936, p. 321
	2 Rocky plateau, Akpatok Island, Ungava Bay, Canada	23	3	—	—	—	—	29	26	1.12	88	79	
Arctic heath	3 <i>Cassiope tetragona</i> heath, Wijde Bay, West Spitsbergen	21	3	1	—	—	—	30	25	1.20	84	70	Summerhayes & Elton, 1928, p. 235
Subarctic heath	4 Better vegetated slopes of ravines, Akpatok Island, Ungava Bay, Canada	26	5	1	—	—	—	39	32	1.22	81	67	Davis, 1936, p. 325
Subarctic scrub	5 Heath (excluding willow scrub), Godthaabsfjord, West Greenland	56	7	1	1	—	—	77	65	1.19	86	73	Longstaff, 1932, p. 122
	6 Willow (<i>Salix glauca</i>) scrub, Godthaabsfjord, West Greenland	34	6	2	2	—	—	60	44	1.36	77	57	Longstaff, 1932, p. 126
Temperate grassland	7 Invertebrates of soil and surface vegetation, meadow on clay, near Oxford, England	61	11	2	1	—	—	93	75	1.24	81	66	Ford, 1935, p. 198
Temperate woodland	8 Invertebrates in logs (complete succession, several years), Duke Forest, North Carolina:	92	8	1	—	—	—	111	101	1.10	91	83	Savely, 1939, pp. 377, 381
	9 <i>Pinus taeda</i> and <i>echinata</i> logs	118	6	2	—	—	—	136	126	1.08	94	87	
Subarctic bog	10 <i>Quercus alba</i> , <i>borealis</i> (= <i>rubra</i>), <i>velutina</i> and <i>stellata</i> logs	17	2	—	—	—	—	21	19	1.11	89	81	Longstaff, 1932, p. 131
Temperate fresh-water pond	11 West Greenland	26	3	—	—	—	—	32	29	1.10	90	81	Davis, 1936, p. 324
	12 Bog and pool margins, plateau valley, Akpatok Island, Ungava Bay, Canada	21	4	1	—	—	—	32	26	1.23	81	66	Pyefinch, 1937, p. 128
Temperate lake benthos	13 General fauna of 8 fresh-water ponds, Bardsey Island, north Wales	61	8	1	1	0	1	90	72	1.25	85	68	Laurie, 1942, p. 172
	14 Moorland hill pond, rich vegetation, Wales	38	6	0	1	1	—	59	46	1.28	83	64	Humphries, 1936, p. 32
	15 Ditto, profundal	6	1	0	0	1	—	13	8	1.63	75	46	Ditto

Table 1 (continued)

General habitat	Community	No. of genera with the following nos. of species present						Total no. of species analysed (B)	Total no. of genera analysed (C)	Average no. of species per genus (B/C)	% of genera with one species present (A/C)	% of 'single species' present (A/B)	Reference
		1 (A)	2	3	4	5	6						
Temperate lake	16 Invertebrates, sublittoral 10-40 m., Vättern (cold relict fresh-water lake), Sweden	44	8	1	3	1	1	86	58	1.51	76	51	Ekman, 1915, p. 373
Temperate lake, zoo-plankton	17 Lac de Bret, Switzerland, altitude 673 m.	22	3	1	—	—	—	31	26	1.19	85	71	Linder, 1904, p. 166
	18 Lake Washington, Washington, near sea-level	18	8	—	—	—	—	34	26	1.31	69	53	Scheffer & Robinson, 1939, p. 117
	19 Lake Michigan (Great Lakes): (a) 1887-8 (b) 1926-7	21	8	1	—	—	—	40	30	—	70	52	Eddy, 1927, p. 212
	Average	19	6	1	—	—	—	34	26	—	73	56	
Temperate river	20 Invertebrates, River Wharfe, Yorkshire	20	7	1	—	—	—	37	28	1.32	71	54	Percival & Whitehead, 1930, p. 296
	21 Invertebrates and fish, River Lark, East Anglia	82	7	6	3	1	—	131	99	1.44	83	63	Butcher, Pentelow & Woodley, 1931, p. 103
	22 Invertebrates, fish and Amphibia, River Rheidol, Wales (recovering from lead pollution)	42	5	1	1	0	1	65	50	1.30	84	65	Laurie & Jones, 1938, p. 280
	23 Ditto, River Melindawr, Wales (Stations A-F, lead pollution)	47	6	3	1	0	1	87	59	1.47	80	54	Jones, 1940a, p. 193
	24 Ditto, River Dovey, Wales (no pollution)	46	4	3	0	1	—	68	54	1.26	85	68	Jones, 1941, p. 18
Temperate estuary	25 Invertebrates, River Ystwyth, Wales (zinc pollution; no fish or molluscs)	81	16	5	—	—	—	128	102	1.25	79	63	Jones, 1940b, p. 374
	26 Plankton, River Thames, South-end, 5 years	43	4	1	0	1	—	59	49	1.20	88	73	Wells, 1938, p. 116
	27 Benthos and a few plankton invertebrates and the fish, River Tamar, Devonshire. (Upper salinity at stations, 0.06‰-25.3‰)	56	5	3	1	—	—	79	65	1.22	86	71	Percival, 1929, p. 95
Arctic marine drift-line	28 Intertidal and bottom benthos, River Tay, Scotland	49	4	1	—	—	—	60	54	1.11	91	82	Alexander, 1932, p. 37
Subarctic marine drift-line	29 Invertebrates and birds, Reindeer Peninsula, West Spitsbergen	89	5	2	—	—	—	105	96	1.19	93	85	Summerhayes & Elton, 1928, p. 250
Subarctic marine drift-line	30 Invertebrates, Godthaabsfjord, West Greenland	12	3	1	—	—	—	21	16	1.31	75	57	Longstaff, 1932, p. 134
Subarctic marine intertidal	31 Invertebrates, Amerdloq Fjord, west Greenland: (a) Rock (b) Sand (c) <i>Mytilus</i> beds (a-c) Three types combined	19	2	—	—	—	—	23	21	1.10	90	83	Steven, 1938, p. 61
	(a) Rock	14	1	—	—	—	—	16	15	—	93	87	
	(b) Sand	5	—	—	—	—	—	5	5	—	100	100	
	(c) <i>Mytilus</i> beds	33	2	—	—	—	—	37	35	—	94	89	
	(a-c) Three types combined	33	2	—	—	—	—	37	35	1.06	94	89	

Temperate marine intertidal	32	Invertebrates, rocky shore, Plymouth, England (4 years after colonization began)	54	3	1	1	0	1	—	73	60	1:22	90	74	Moore & Sproston, 1940, p. 61
	33	Invertebrates and fish, sand shore, Port Erin Bay, Isle of Man	17	—	—	—	—	—	—	17	17	1:00	100	100	Pirrie, Bruce & Moore, 1932, p. 287
	34	Invertebrates and fish, rocky shore (excluding rock-pools), Bardsey Island, Wales	85	10	1	—	—	—	—	108	96	1:12	88	79	Pyefinch, 1943, p. 84
	35	Wharf piles, Wood's Hole, Massachusetts	74	8	3	—	—	—	—	99	85	1:17	87	75	{ Allee, 1923, pp. 213, 218
Tropical marine intertidal	36	Exposed rocks, ditto	50	4	3	—	—	—	—	67	57	1:18	88	75	Stephenson <i>et al.</i> , 1931, p. 44
	37	Coral reef flat, Low Isles, Great Barrier Reef, Australia	50	5	3	—	—	—	—	69	58	1:19	86	72	
Temperate marine benthos	38	Dogger Bank, North Sea, (a) 150 stations [Voyage 48]	38	9	—	—	—	—	—	56	47	1:19	81	68	Davis, 1923, p. 9
	39	Ditto, (b) smaller area (900 sq. miles), 100 stations [Voyages 22, 26, 29]	35	4	—	—	—	—	—	43	39	1:10	90	81	Ditto
	40	Ditto, (c) still smaller area (340 sq. miles), 189 stations [Voyage 39]	29	2	—	—	—	—	—	33	31	1:06	94	88	Ditto
Temperate marine zoo-plankton	41	Shields area, Northumberland, North Sea [Stations 14-30]	39	3	—	—	—	—	—	45	42	1:07	93	87	Savage, 1926, Table 3
Parasite faunas	42	Endoparasites, salamander, <i>Desmognathus fuscus</i> , stream and swamp-stream margin in woodland, lower Piedmont, North Carolina	13	2	—	—	—	—	—	17	15	1:13	87	76	Rankin, 1937, p. 184
	43	Endoparasites, salamander, <i>Plethodon cinereus</i> , oak-hickory forest, above streams, Blue Ridge Mountains, North Carolina	9	1	—	—	—	—	—	11	10	1:10	90	82	Ditto
	44	Ectoparasites, wood-mouse, <i>Apodemus sylvaticus</i> , Bagley Wood, Oxford	17	1	—	1	—	—	—	23	19	1:21	89	74	Elton, Ford, Baker & Gardner, 1931, p. 706, etc.
	45	Ditto, endoparasites	16	1	—	—	—	—	—	18	17	1:06	94	89	Ditto, p. 683, etc.
	46	Nest fauna of wild house-mouse (<i>Mus musculus</i>) (parasites and other inhabitants), Isle of Lewis, Outer Hebrides	13	2	—	—	—	—	—	17	15	1:13	87	76	Elton, 1934, p. 109
	47	Ecto- and endoparasites of brown rat (<i>Rattus norvegicus</i>), England	20	1	1	—	—	—	—	25	22	1:14	91	80	Balfour, 1922, p. 290
	48	Ecto- and endoparasites, steppe ground squirrel (<i>Citellus pygmaeus</i>), South-east Russia	23	2	1	—	—	—	—	30	26	1:15	88	77	Sassuchin & Tiflow, 1933, p. 438
	49	Ecto- and endoparasites, cotton-tail (<i>Sylvilagus floridanus mallurus</i>), Durham County, North Carolina	10	1	—	—	—	—	—	12	11	1:09	91	83	Harkema, 1936, p. 160
Totals (49 units)			1912	225	55	17:25	6:25	5	1	2666:25	2221:5	1:38	86	72	
%			86:07	10:13	2:48	0:78	0:28	0:22	0:04						

birds, etc. But within the groups collected analysis can be made, provided a high proportion of the genera have all their species identified.

(4) It is more important that a number of groups should have been collected completely and separated into reliable species, than that all groups should be recorded. A good many lists that were insufficiently broken down into species had to be omitted. I have, however, accepted certain surveys, mostly fresh-water benthos ones, that record 'species *a*, *b*', etc., without actual Latin names; most of these being immature stages not yet correlated with known adult species. It will be realized, therefore, that the 'total number of species analysed' in Table 1 is seldom the total number present on the area, and is usually a little less than the total number given in the published surveys. Some of the detailed decisions that had to be made are relegated to an Appendix.

Table 2. *Frequency distribution of the percentages of genera with only one species present, in forty-nine animal communities*

Percentage	66-	71-	76-	81-	86-	91-	96-
No.	1	4	4	11	18	10	1

Table 3. *Frequency distribution of the percentages of 'single species' present, in forty-nine animal communities*

Percentage	46-	51-	56-	61-	66-	71-	76-	81-	86-	91-	96-
No.	1	4	3	4	7	9	6	9	5	0	1

(5) Although these communities are treated as if they are a random sample, they do include most of the reliable and fairly complete surveys known to me (except that, in order to retain some balance between different types of habitat, the proportion of European fresh-water surveys is not high). Also, although the percentages are all grouped together into one frequency table (Table 2), it will probably turn out, when enough surveys have accumulated, that some major habitats will show figures consistently higher or lower than the average. At present too few reliable surveys exist to decide whether such differences are really present in the ecosystems concerned, or whether they are inherent in the collecting methods or even in the taxonomic conventions for particular groups.

(c) *Plant communities*

Only a small sample analysis of plant communities is given here (Table 4), out of the very large published material that exists. No special selection was exercised in the choice of twenty-seven communities for analysis, provided they were complete and on clearly defined habitat areas and the lists were local rather than very large regional ones, except that the samples were intended to cover a wide range of conditions. It is sufficient to prove that the genus/species relationships are similar to those in animal

communities: the frequencies summarized in Table 4 are remarkably similar to those in Table 2, e.g. the average percentage of genera with only one species present is 84 (range 63-96), compared with 86 for animal communities, and the average number of species per genus 1.22 (range 1.06-1.47), compared with 1.38 for animal communities. The almost exact correspondence of these averages may be partly a coincidence, but considering the very wide range of communities analysed, the resemblances are certainly remarkable and would lead one to suppose that there is some common principle operating both for plants and animals. The agreement is important also because most plant ecological surveys are more complete than animal ones, and because we know by direct evidence something of the direct competition that exists between plant species.

2. DISCUSSION AND WORKING HYPOTHESIS

(a) *Faunal statistics*

One possible explanation of the statistical relationships described above would be that the frequencies

of species in genera simply reflect those of the fauna as a whole. For if, say, 86% of species in the British Isles belonged to genera of which only one species was present in this region, the figures in Tables 1 and 4 would be the record of a faunistic distribution, rather than of any peculiarity of homogeneous communities taken separately. Since insects form a high proportion of the fauna on land and in fresh water, we can take the British insect fauna as a test of this question, using the recently published 'Check list of British insects' (Kloet & Hincks, 1945), in which the numbers of established genera and species are summarized for each order (or in some cases, suborder). In Table 5 these thirty-one insect groups are arranged in ascending series of size, the Hemiptera being split into four, the Hymenoptera into six, and the Diptera into two subgroups. The frequencies for different groups are given in Table 6, with those of the animal communities for comparison. Whereas all the community figures for the number of species per genus lie in the frequency class 1.00- (actually, 1.00-1.63), only about 10% of those for the insect groups are in that class, and their percentages range from this to over 7.00. Although the greatest frequencies lie in the classes 2.00- to 4.00-, with a peak in 2.00-, the weight of the very large insect groups Hymenoptera, Lepidoptera, Diptera and Coleoptera (which together form 84% of the total British insect

species and which all have high ratios) brings the average for the whole assemblage of insect groups to 4.23.

Since Kloet & Hincks seem to have inclined rather strongly towards the splitting of genera (i.e. calling subgenera genera) and the ecological surveys analysed here were done at earlier periods when generic splitting in most groups had gone less far, it may safely be stated that, *on the average*, for every species of insect present in a British animal community there are at least three or four others of the same genus

for the eleven largest groups, the percentages being given in the fourth column of Table 5. They range from 28 to 57%, but most of them lie between 44 and 57%, and the average for the whole lot is 50%. This is the figure that we may compare with 86% for the animal communities. The differences between particular communities and the fauna as a whole are evidently considerable in this respect, whether we consider the average number of species per genus or the percentage of genera with 'single species'. The difference is greater for the former figure than for

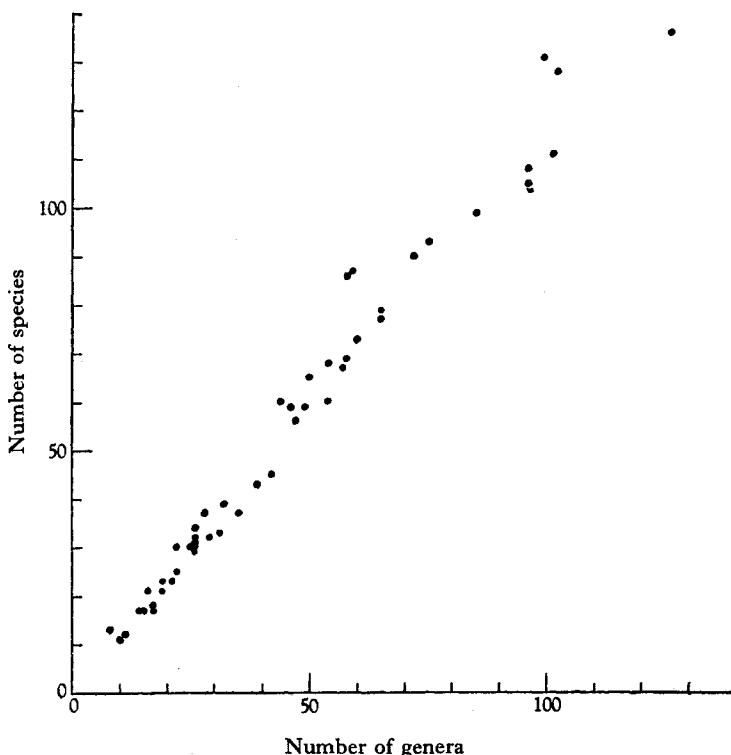


Fig. 1. Relation between the number of species and the number of genera present in forty-nine animal communities (from Table 1).

present in the country. But in the communities considered, the average number of species per genus was only 1.38, i.e. *on the average* every species only had two-fifths of another species living with it. This comparison is not quite satisfactory, because the insect statistics refer only to the insect groups of a fairly typical temperate continental island, while the community figures are derived from a very wide sample of varied animal groups from habitats in the Northern Hemisphere; but I think it illustrates a real difference that will be generally found to occur.

The Check List does not summarize the numbers of monospecific genera. I have therefore done this

the latter, owing to the presence in the general faunal lists of a great many large genera, with numbers far exceeding the usual limit of three or four found in the community lists.

It can still be said that the community statistics might be reflecting the general fauna picture for a smaller region within a country. I have considered making a further check by analysing the lists of county faunas, such as those published in the *Victoria County Histories*, but came to the conclusion that the comparison would probably be meaningless, because these lists are compiled over a very long period of time and do not necessarily describe the fauna of

Table 4. Analysis of genus/species relations in twenty-seven plant communities

General habitat	Community	No. of genera with the following nos. of species present						Total no. of species analysed (B)	Total no. of genera analysed (C)	Average no. of species per genus (B/C)	% of genera with one species present (A/C)	% of 'single species' present (A/B)	Reference
		1 (A)	2	3	4	5	6						
Arctic fjeldmark	1 Frost-weathered rocky soil, Bear Island	16	4	1	1	—	—	31	22	1.41	73	52	Summerhayes & Elton, 1923, p. 220
	2 Rocky lowland (non-polygon soil), Prince Charles Foreland, Spitsbergen	24	5	3	—	—	—	43	32	1.34	75	56	Ditto, p. 244
Arctic heath	3 <i>Cassiope tetragona</i> heath, Wijde Bay, West Spitsbergen	28	7	0	1	1	—	51	37	1.38	76	55	Summerhayes & Elton, 1928, p. 233
Subarctic heath	4 <i>Empetrum-Betula nana</i> heath, Billefjordelv area, Finnmark, Norway	26	3	2	1	—	—	42	32	1.28	81	62	Leach & Polunin, 1932, p. 420
	5 Drier <i>Betula odorata</i> forest, same area as (4)	24	1	1	—	—	—	29	26	1.12	92	83	Ditto, p. 417
Temperate grassland	6 Nardetum, Cader Idris, north Wales	20	3	—	—	—	—	26	23	1.13	87	77	Evans, 1932, p. 25
	7 <i>Deschampsia flexuosa</i> grass heath, Bunter sandstone, Nottinghamshire, England	42	10	1	0	1	—	70	54	1.30	78	60	Hopkinson, 1927, p. 159
Steppe	8 Primitive chalk grassland, Buriton, West Sussex, England	52	10	2	1	—	—	82	65	1.26	80	63	Tansley & Adamson, 1925, p. 185
	9 <i>Avena desertorum</i> meadow steppe, Kuznetszk District, Saratov, Russia	46	8	2	—	—	—	68	56	1.21	82	68	Keller, 1927, p. 220
Temperate scrub	10 Limestone heath-scrub, Ballyvaghan, Co. Clare, Ireland	25	0	1	—	—	—	28	26	1.08	96	89	Tansley, 1939, p. 474
Temperate carr	11 Open carr, Esthwaite Fens, Lake District, England	50	5	2	0	0	1(7)	73	58	1.26	86	68	Pearsall, 1918, p. 61, summarized by Tansley, 1939, p. 644
	12 Valley fenwoods, River Lark, East Anglia, England	35	5	3	1	—	—	58	44	1.32	80	60	Farrow, 1915, p. 226, summarized by Tansley, 1939, p. 467
	13 Coppiced alder carr, Cothill, Berkshire, England	38	4	0	1	—	—	50	43	1.16	90	76	Tansley, 1939, p. 469
	14 Alder carr, Wheatfen Broad, Norfolk, England	47	9	1	1	—	—	72	58	1.24	81	65	Ellis, 1935, summarized by Tansley, 1939, p. 461

Temperate woodland	15	Ashwood, Ling Ghyll, Yorkshire, England	50	8	2	—	—	—	—	72	60	1:20	83	69	Tansley, 1939, p. 433 Ditto, p. 344
		Highland oakwood, Scotland:													
	16	(a) Portclair (<i>Quercus robur</i>)	38	4	—	—	—	—	—	46	42	1:10	90	83	
	17	(b) Loch Leven (<i>Q. sessiliflora</i>)	49	3	—	—	—	—	—	55	52	1:06	94	89	
	18	Birchwood, Cader Idris, north Wales, 800-1100 ft.	40	5	—	—	—	—	—	50	45	1:11	89	80	Evans, 1932, p. 20
	19	Mature beechwood (serie 1, stage 3), Singleton Forest, Sussex Downs, England	39	3	—	—	—	—	—	45	42	1:07	93	87	Watt, 1925, p. 50
	20	Red fir forest, Sierra Nevada, California	60	12	3	—	—	—	—	93	75	1:24	80	64	Oosting & Billings, 1943, p. 271
Temperate lake plankton	21	Windermere, England	18	1	0	1	—	—	—	24	20	1:20	90	75	Pearsall, 1932, p. 261
Temperate lake littoral	22	Phanerogams, Lake Mendota, Wisconsin	13	1	0	0	1	—	—	21	15	1:40	87	62	Denniston, 1921, p. 500
Subarctic marine intertidal	23	Amerdloq Fjord, West Greenland	10	1	—	—	—	—	—	12	11	1:09	91	83	Steven, 1938, p. 62
Temperate marine intertidal	24	Rocky shore, Plymouth, England (4 years after colonization)	12	1	—	—	—	—	—	14	13	1:08	92	86	Moore & Sproston, 1940, p. 319
Tropical marine intertidal	25	Coral reef flat, Low Isles, Great Barrier Reef, Australia	12	5	2	—	—	—	—	28	19	1:47	63	43	Stephenson <i>et al.</i> , 1931, p. 45
Marine phytoplankton	26	Aberystwyth Harbour, Wales	18	1	1	—	—	—	—	23	20	1:15	90	78	Lloyd, 1925, p. 103
	27	Shields Area, Northumberland, North Sea [Station 26]	7	1	0	1	—	—	—	13	9	1:45	78	54	Savage, 1926
		Totals (27 units)	839	120	27	9	2	1	1	1219	999	1:22	84	69	
		%	83.99	12.01	2.70	0.90	0.20	0.10	0.10						

a region in one year or a short period of years; whereas the community surveys are done usually within a year or at most a few years. Nevertheless, the faunal list does indicate the species that either live or have attempted to live within the area, and it is notable that 54% of the British species of Hemiptera Heteroptera have been recorded from an area as small as the county of Oxfordshire (China, 1939) and

conclusions drawn here. But although the list of habitats is an extremely varied one and gives a very wide sampling, it is deficient (except for no. 7, Table 1) in one very important class of animal community, that of terrestrial habitats of temperate and tropical regions containing complex plant associations. The reason for this omission is, of course, the absence of sufficiently complete surveys hitherto.

Table 5. *Relation between the number of genera and of species in thirty-one British insect orders or suborders (established species), columns 1 and 2 from Kloet & Hincks (1945)*

Order	No. of species	No. of genera	No. of species per genus	% of genera with only one species present
Mecoptera	4	2	2.00	—
Megaloptera	6	3	2.00	—
Dermaptera	9	7	1.29	—
Protura	17	4	4.25	—
Strepsiptera	17	5	3.40	—
Thysanura	23	7	3.29	—
Plecoptera	32	15	2.13	—
Orthoptera	38	27	1.41	—
Odonata	42	21	2.00	—
Ephemeroptera	46	19	2.42	—
Siphonaptera	47	24	1.96	—
Neuroptera	54	18	3.00	—
Psocoptera	68	33	2.06	—
Hemiptera, Coccoidea	103	38	2.71	—
Thysanoptera	183	42	4.35	—
Trichoptera	188	70	2.69	—
Hymenoptera, Cynipoidea	228	49	4.65	—
Collembola	261	62	4.21	—
Anoplura (including Mallophaga)	286	73	3.92	—
Hemiptera, Aphidoidea	375	122	3.07	—
Hymenoptera, Symphyta	430	92	4.67	35
Hemiptera, Homoptera	434	92	4.71	46
Hemiptera, Heteroptera	499	221	2.26	57
Hymenoptera, Aculeata	531	139	2.82	44
Hymenoptera, Proctotrupoidea	613	93	6.60	28
Hymenoptera, Chalcidoidea	1564	214	7.31	51
Diptera, Cyclorrhapha	2072	652	3.18	53
Lepidoptera	2187	657	3.33	57
Hymenoptera, Ichneumonoidea	2825	485	5.82	44
Diptera, Orthorrhapha	3127	480	6.53	45
Coleoptera	3690	947	3.90	50
Total insects*	19999	4713	4.23	
Average (from raw totals, 11 groups)				50

* Omitting 25 'Addenda' to the list.

that Waters (1929) found that at least 58% of the British species of micro-Lepidoptera had been recorded within seven to ten miles of Oxford.

(b) *Limitations of the community data*

It was pointed out in § 1 that the community surveys analysed are certainly incomplete in many respects, but that the features in which they themselves were lacking were not likely to invalidate the

On the whole, the list given in Table 1 contains animal communities in which the species live on a comparatively few different basic sources of food. This applies to log-dwelling herbivores, which depend on phloem, on fungi growing in the galleries made by the phloem-eaters, and on the wood (Savely, 1939); to soil animals; to fresh-water, estuarine and marine bottom detritus or plankton feeders; to intertidal animals dependent on plankton; to zooplankton

itself; to drift-line animals eating decaying matter; and to blood-sucking ectoparasites. I do not mean that there is no ecological differentiation in the food habits of species living, say on phloem in logs or mud on the sea bottom; only that this type of community consists mainly of a few ecological groups each broadly drawing upon the same natural resources for its basic food, with of course the usual predator-parasite food cycle rising from it.

Even in those aquatic habitats that have a number of plant species (e.g. fresh-water benthic phanerogams, intertidal sea-weeds, and phytoplankton) few of the herbivores seem to be restricted to one or a few plant species. The same thing applies in general to Arctic and Subarctic terrestrial communities, where specialization of herbivores is rather exceptional.

mostly species pairs—also show strong ecological differences in habits, although they live within the same community. Lack's study (1944) of passerine birds has brought this point out especially clearly. He also gives many instances of genera whose species are split up between different major habitats. In other instances, although we have not yet got any direct evidence of different habits or tolerance ranges, quantitative survey shows one species of a pair to be much more abundant than another. Thus in his Dogger Bank samples Davis (1923, Voyage 48) got 1182 specimens of the lamellibranch *Spisula subtruncata*, and only four of *S. solida*. These appear, however, as a species pair in Table 1 of the present paper. Undoubtedly some other 'species pairs' will be due to chance immigration of one species not living in that habitat, but these (as also instances of

Table 6. Frequency distributions of numbers of species per genus in (a) forty-nine animal communities (b) thirty-one British insect orders or suborders

	1·00-	2·00-	3·00-	4·00-	5·00-	6·00-	7·00-
No. of communities	49	—	—	—	—	—	—
% of communities	100	—	—	—	—	—	—
No. of orders or suborders	3	10	8	6	1	2	1
% of orders or suborders	9·7	32·3	25·8	19·4	3·2	6·4	3·2

The situation in highly organized terrestrial communities like heath, meadow, scrub and woodland is different. Here we find large numbers of monophagous species, especially among insects, attached to particular plant species. Since there may be commonly up to seventy species of plants in one association, the majority of which are phanerogams edible to some animals, the possibilities for ecological differentiation within the community are therefore much greater than in communities of the type so far surveyed with any completeness. Such terrestrial communities do not cover a larger area of the globe than ones of the simpler trophic type, but they do contain some of the most highly organized and complicated relationships known between species, and I wish to make it quite clear that the conclusions that follow should be treated as an approach to the more complex problem, through the evidence for simpler communities that has already been accumulated in the short time that animal ecology has been a science.

(c) Ecotypic differentiation

It is already well known that ecotypic differentiation occurs between many species of the same genus. What this community analysis shows is that the amount of differentiation is apparently very high, and that it is a prominent feature of all the communities for which we have sufficient knowledge to make the analysis. There is no doubt that some of the 14 % of genera that have more than one species present—

temporary establishment) might also apply to the single species, and we cannot therefore make any statistical proviso from them. It can be concluded that the amount of ecotypic differentiation in genera is really very high in communities of the type we are considering here, and that it is the exception to find groups of species of the same genus occupying the same ecological niche on the same area or apparently doing so (as does, however, occur in genera like the lamellibranch *Pisidium* or the larvae of the black-fly *Simulium* in fresh water).

(d) Competition and community structure

Ecological research has discovered a good deal about the 'vertical' organization of animal communities. By 'vertical' I mean here, not vertical layering of the habitat, but the flow of matter and energy through different levels of consumption, as found in food chains, with their herbivore-plant, predator-prey, parasite-host and other relationships; fluctuating equilibrium between the stages in these chains; cover, making such equilibrium possible; daily and other activity rhythms causing alternating mass action of different components of the community in response to environmental cycles; and the ultimate limit (usually about five stages) set to the number of consumer levels by the size relations of animals and the pyramid of numbers. In this field of ecology it is possible to proceed with some general measure of agreement on the fundamental principles at work

(see Lindeman, 1942, who has restated the subject in a useful essay).

We also have a great deal of information, though none of it complete in respect to any single species, about the tolerance ranges, optima and preferences that animals have in regard to various habitat factors like temperature, humidity and amount and quality of food—the ranges, etc. often varying with the sex and life history stage of the species and with the type of life process (growth, viability, reproduction, activity, etc.) studied. Here again, research is progressing along well-defined lines, though still very weak upon the fundamental problem of habitat selection in nature.

When we come to the 'horizontal' organization of animal communities, i.e. the dynamic relations between species of the same consumer level, we find that little is known except from very simplified laboratory experiments and from certain lines of *a priori* reasoning. The pros and cons of argument on this question were partly explored in the British Ecological Society's Symposium (21 March 1944) on 'The ecology of closely allied species' (Anon. 1944), at which the substance of the present paper was put forward for discussion. But that discussion was mainly concerned with closely allied forms, whereas I wish to consider now the relation between all species of the same genus. The statistics of Table 1, and the field lists on which they are based, really mean that these animal communities have, at each level of consumption (i.e. food-chain stages 1, 2, 3, 4, ...) a certain number, from several to a score or more, of species that mainly belong to separate genera. These, as has been indicated, could be broken up into subgroups each drawing its food from a common pool, though not necessarily from exactly the same part of it at the same time, or in the same way.

We simply do not understand exactly why populations of, say, a Pentatomid bug, a grasshopper, a moth caterpillar, a vole, a rabbit and an ungulate should be able to draw upon the same common resource (grassland vegetation) and yet remain in equilibrium at any rate sufficiently to form a stable animal community over long periods of years. In all communities the primary resources of plant or decaying matter (or with parasites, tissues or the food of the host) are split up in this way between a number of species, each of which is able to maintain, though with fluctuating equilibrium, its own share of the common natural resource. I think it has usually been assumed, by analogy with the specific food habits of monophagous or not very polyphagous insects, that the equilibrium is made possible by some specialized division of labour, and that the animals do not come into direct competition at all; or else that the amount of resources is generally sufficient to provide for all

the populations present because they are limited by factors other than food in the increase of their populations. The second idea is on the whole supported by the general evidence that animals do not normally become limited in numbers by starvation, and that the biomass of phanerogamic vegetation is far beyond that of animals dependent on it. However this may be, we know extremely little about the whole subject.

Darwin, in *The Origin of Species*, remarked that 'As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera. We see this in the recent extension over parts of the United States of one species of swallow having caused the decrease of another species. The recent increase of the missel-thrush in parts of Scotland has caused the decrease of the song-thrush. How frequently we hear of one species of rat taking the place of another species under the most different climates! In Russia the small Asiatic cockroach has everywhere driven before it its great congener. One species of charlock will supplant another, and so in other cases. We can dimly see why the competition should be most severe between allied forms, which fill nearly the same place in the economy of nature; but probably in no one case could we precisely say why one species has been victorious over another in the great battle of life.'

More recently, Gause (1934) and other laboratory workers have shown by experiments in controlled environments how one of two similar species of a genus introduced into a culture will prevail eventually over the other. That this type of competition is not confined to species of the same genus is well proved by the experiments of Crombie (1945, 1946) with grain insects, in which a beetle was able eventually to crowd out a moth, both having larvae living inside the grains of wheat; also in similar experiments with beetles by Park, Gregg & Lutherman (1941). Here competition was effective between members of two different orders of insects, and we have the type of equilibrium problem that is most commonly encountered in the field. The importance of the community analysis given in the present paper is that it confirms the general proposition that some (though not necessarily all) genera of the same consumer level that are capable of living in a particular habitat at all can coexist permanently on an area; whereas it is unusual, in the communities analysed, for species of the same genus to coexist there. We therefore arrive at some points for a working hypothesis to cover our present limited knowledge of competition in relation to basic community structure.

It should be stressed that 'competition' is here used not merely for direct antagonism or struggles for space, etc., but as an objective description (in the same way that 'natural selection' or the 'struggle for existence' are only shorthand terms) of the interplay of longevity and fertility factors of all kinds (known and unknown) favouring one species at the expense of another.

(1) Every habitat that supports a whole community of animal species contains one or more pools of natural resources available for the building up of animal populations, plant resources (alive or dead) being usually the most immediately important, and in all cases the ultimate source there or elsewhere.

(2) In habitats where there are not large numbers of terrestrial plant species suitable for food specialization by animals (i.e. most of those considered in Table 1), these resources are exploited for the greater part by genera with only one species present on that area of habitat, genera with more than two species present forming a small fraction only. Very large genera do not seem to be represented in full force at all. The main extra-specific ecological relations in such communities are between organisms with generic differences.

(3) We do know a little, experimentally and from field observations (especially on introduced species and their allies) about the effectiveness of competition between species of the same genus. We also know that similarly effective competition can occur between species of separate genera, or even orders. We do not at present know what maintains the state of equilibrium between the different genera actually found in the natural communities analysed, but must postulate that there is some ecological condition that buffers or cuts down the effectiveness of competition between species separated by generic characters. This problem is therefore seen to be the central problem in animal community structure, because it is the variety of species that can coexist at the primary consumer level, that makes possible the considerable complexity of the superstructure of secondary and other consumers.

(4) The comparative shortness of the lists in the community surveys analysed suggests that on any one area of a given habitat, there is in fact restriction upon the number of primary consumers that can coexist (see Elton, 1933), and that there is therefore also some real state of population competition or tension between the different primary consumers, just as there is known to be between primary producers in plant communities.

There is a point about competition that has perhaps not yet been brought out clearly in this discussion. It does not follow that because we find only one species of a certain genus living in a particular animal community on a particular area,

that this is the only species of that genus that is capable of living in that habitat. In other words, we have to distinguish carefully between ability to live in a habitat and ability to live among a particular assemblage of other species present there. There may be lists of species, though usually short ones, of the same genus, all capable of contending with the habitat conditions (tundra, marine intertidal, etc.), but it may still be true that only one (or not often more than two) of them can coexist permanently on the same area of it. So we might not be surprised to find a given niche occupied in one area by one species and in another area of the same general habitat by another. Such differences in distribution might either be due to minor variations in the habitat that we have perhaps not yet detected, or they might be due to the process of competition that has been postulated.

The laboratory experiments of Park *et al.* (1941) illustrate the working of such a situation between two species of beetles, *Tribolium confusum* and *Gnathocerus cornutus* of the same family Tenebrionidae, competing for a common food supply of ground cereals and yeast, but each cannibalizing the early stages of the other species. Competition was well marked between these two species, but the end result depended partly upon the relative initial densities of the two forms. It was possible to get pure or almost pure cultures of either species developing from cultures that had been initially mixed. In nature we might expect to find a number of instances of this happening between species of the same genus, although all the species concerned might be found in some area or other of the general habitat under observation. In discussing the statistical picture of communities given in the present paper, it is therefore essential to remember that each survey was made on a relatively (though not always absolutely) small area of the total habitat.

Finally, something must be said about current trends in taxonomic methods, and especially about fashions for lumping or splitting genera, for these will have a good deal of influence in future handling of community statistics of the type we have been considering. Practically all the animal surveys in Table 1 were done in the 20 years 1921-40, and their nomenclature is a random sample of the taxonomic practices, fashions, advances and retreats, and equilibria of group specialists in various countries during that period and before it. No doubt a good deal of the differences in the frequency pictures for different surveys can be attributed to these variations in taxonomic treatment. Future comparisons will have to take into account the marked tendency for further splitting of genera in many groups of animals, and in some plants, with the reduction in average numbers of species per genus that this involves, and increase

in number (though not always necessarily in the percentage) of monotypic genera. I believe that further research on community structure will eventually give us some new, ecological, criteria for generic classification.

3. ACKNOWLEDGEMENTS

I would like to thank Captain Cyril Diver, Mr David Lack and Mr P. H. Leslie for stimulus and help, and some modifying ideas, given during discussions of these problems during the last two years.

4. SUMMARY

1. Analysis was made of the published ecological surveys of fifty-five animal (including some parasite) communities and twenty-seven plant communities from a wide range of habitats, and the frequencies of genera with different numbers of species tabulated. A rather constant and high percentage of genera with only one species present was found, the average being 86% for animal and 84% for plant communities. The corresponding average numbers of species per genus were 1.38 and 1.22.

2. These figures differ considerably from those of a faunal list for any large region, e.g. the percentage of genera with only one species present for eleven

large British insect groups is 50, and the average number of species per genus for all British insects is 4.23.

3. The difference in species/genus frequencies between ecological surveys of relatively small parts of any general habitat, and those for faunal lists from larger regions, is attributed to existing or historical effects of competition between species of the same genus, resulting in a strong tendency for the species of any genus to be distributed as ecotypes in different habitats, or if not, to be unable to coexist permanently on the same area of the same habitat.

4. These conclusions apply at present only to the list of communities hitherto surveyed with any completeness, which does not include a sufficient sample of terrestrial habitats like heath, meadow, scrub and woodland containing many plant species. The animal communities analysed are mostly ones in which the primary consumer species depend on only a few natural resources.

5. The ability of certain groups of species, mostly separated by generic characters, to exist together on the same area while drawing upon a common pool of resources, is one of the central unsolved problems in animal community structure and population dynamics.

APPENDIX

Special notes on the compilation of Table 1

Community no.	Community no.
1-11	Insect parasites omitted from the table.
1-6	Immigrant adult aquatic flies are included because they are an integral part of the food supply of spiders on land. A part of the micro-fauna of mites and Collembola has probably been omitted from all these surveys, as it requires special methods of collection (see Hammer, 1944).
8-9	Mites omitted from the table.
11	Subgenera of <i>Spamiotoma</i> treated as separate genera, for uniformity with other surveys.
12	Entomostraca omitted from the table, also five records from an earlier survey.
14-15	All Chironomidae genera containing any species just marked 'sp.' or 'gr.' (for group) omitted from the table.
16	The depth taken for sublittoral is slightly arbitrary, as the actual limits vary in different parts of a lake. Chironomidae and most Trichoptera omitted from the table.
	19 Two independent surveys of Lake Michigan were done 40 years apart. There were some significant differences in species, but little in the genera present.
	20 Chironomidae omitted from the table.
	22-23 Diptera omitted from the table.
	26 Fish omitted from the table.
	35-36 Surveys covered 9 years.
	38-40 This survey does not include all bottom-living fish.
	41 Autotrophic flagellates omitted from the table.
	45-47 Spirochaetes and bacteria omitted from the table.
	48 Single records omitted from the table.

REFERENCES

- Allee, W. C. (1923). 'Studies in marine ecology. III. Some physical factors related to the distribution of littoral invertebrates.' Biol. Bull. Wood's Hole, 44: 205-53.
- Alexander, W. B. (1932). 'The natural history of the Firth of Tay.' Trans. Perthshire Soc. Nat. Sci. 9: 35-42.
- Anon. (1944). 'British Ecological Society. Easter meeting 1944. Symposium on "The ecology of closely allied species".' J. Anim. Ecol. 13: 176-8; also in (1945) J. Ecol. 33: 115-16.
- Balfour, A. (1922). 'Observations on wild rats in England, with an account of their ecto- and endoparasites.' Parasitology, 14: 282-98.

- Butcher, R. W., Pentelov, F. T. K. & Woodley, J. W. A. (1931).** 'An investigation of the River Lark and the effect of beet sugar pollutions.' *Minist. Agric. Fish., Fish. Invest. Ser. 1, 3, No. 3: 1-112.*
- China, W. E. (1939).** 'Hemiptera.' In B. M. Hobby, 'Zoology', in 'The Victoria History of the County of Oxford', 1: 69-77.
- Crombie, A. C. (1945).** 'On competition between different species of graminivorous insects.' *Proc. Roy. Soc. B, 132: 362-95.*
- Crombie, A. C. (1946).** 'Further experiments on insect competition.' *Proc. Roy. Soc. B, 133: 76-109.*
- Darwin, C. (1859).** 'On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.' London. P. 76.
- Davis, D. H. S. (1936).** 'A reconnaissance of the fauna of Akpatok Island, Ungava Bay.' *J. Anim. Ecol. 5: 319-32.*
- Davis, F. M. (1923).** 'Quantitative studies on the fauna of the sea bottom. No. 1. Preliminary investigation of the Dogger Bank.' *Minist. Agric. Fish., Fish. Invest. Ser. 2, 6, No. 2: 1-54.*
- Denniston, R. H. (1921).** 'A survey of the larger aquatic plants of Lake Mendota.' *Trans. Wis. Acad. Sci. Arts Lett. 20: 495-500.*
- Eddy, S. (1927).** 'The plankton of Lake Michigan.' *Bull. Ill. St. Nat. Hist. Surv. 17, Art. 4: 203-32.*
- Ekman, S. (1915).** 'Die Bodenfauna des Vättern, qualitativ und quantitativ untersucht.' *Int. Rev. Hydrobiol. 7: 146-204, 275-425.*
- Ellis, E. A. (1935).** 'Wheatfen Broad, Surlingham.' *Trans. Norfolk Norw. Soc. Nat. 13: 422-51.*
- Elton, C. (1933).** 'The ecology of animals.' London, pp. 17-23.
- Elton, C. (1934).** 'Metazoan parasites from mice in the Isle of Lewis, Outer Hebrides.' *Parasitology, 26: 107-111.*
- Elton, C., Ford, E. B., Baker, J. R. & Gardiner, A. D. (1931).** 'The health and parasites of a wild mouse population.' *Proc. Zool. Soc. Lond.: 657-721.*
- Evans, E. Price (1932).** 'Cader Idris: a study of certain plant communities in south-west Merionethshire.' *J. Ecol. 20: 1-52.*
- Farrow, E. P. (1915).** 'On the ecology of the vegetation of Breckland. I. General description of Breckland and its vegetation.' *J. Ecol. 3: 211-28.*
- Ford, J. (1935).** 'The animal population of a meadow near Oxford.' *J. Anim. Ecol. 4: 195-207.*
- Gause, G. F. (1934).** 'The struggle for existence.' Baltimore.
- Hammer, M. (1944).** 'Studies on the Oribatids and Collemboles of Greenland.' *Medd. Grønland, 141, No. 3: 1-210.*
- Harkema, R. (1936).** 'The parasites of some North Carolina rodents.' *Ecol. Monogr. 6: 153-232.*
- Hopkinson, J. W. (1927).** 'Studies on the vegetation of Nottinghamshire. I. The ecology of the Bunter sandstone.' *J. Ecol. 15: 130-71.*
- Humphries, C. F. (1936).** 'An investigation of the profundal and sublittoral fauna of Windermere.' *J. Anim. Ecol. 5: 29-52.*
- Jones, J. R. E. (1940a).** 'The fauna of the River Melindwr, a lead-polluted tributary of the River Rheidol in North Cardiganshire, Wales.' *J. Anim. Ecol. 9: 188-201.*
- Jones, J. R. E. (1940b).** 'A study of the zinc-polluted river Ystwyth in north Cardiganshire, Wales.' *Ann. Appl. Biol. 27: 368-78.*
- Jones, J. R. E. (1941).** 'The fauna of the River Dovey, West Wales.' *J. Anim. Ecol. 10: 12-24.*
- Keller, B. A. (1927).** 'Distribution of vegetation on the plains of European Russia.' *J. Ecol. 15: 189-233.*
- Kloet, G. S. & Hincks, W. D. (1945).** 'A check list of British insects.' Stockport.
- Lack, D. (1944).** 'Ecological aspects of species-formation in passerine birds.' *Ibis, 86: 260-86.*
- Laurie, E. M. O. (1942).** 'The fauna of an upland pond and its inflowing stream at Ystumtuen, North Cardiganshire, Wales.' *J. Anim. Ecol. 11: 165-81.*
- Laurie, R. & Jones, J. R. E. (1938).** 'The faunistic recovery of a lead-polluted river in North Cardiganshire, Wales.' *J. Anim. Ecol. 7: 272-89.*
- Leach, W. & Polunin, N. (1932).** 'Observations on the vegetation of Finmark.' *J. Ecol. 20: 416-30.*
- Lindeman, R. L. (1942).** 'The trophic-dynamic aspect of ecology.' *Ecology, 23: 399-418.*
- Linder, C. (1904).** 'Étude de la faune pélagique du Lac de Bret.' *Rev. Suisse Zool. 12: 149-258.*
- Lloyd, B. (1925).** 'Marine phytoplankton of the Welsh coasts, with special reference to the vicinity of Aberystwyth.' *J. Ecol. 13: 92-120.*
- Longstaff, T. G. (1932).** 'An ecological reconnaissance in West Greenland.' *J. Anim. Ecol. 1: 119-42.*
- Moore, H. B. & Sproston, N. G. (1940).** 'Further observations on the colonization of a new rocky shore at Plymouth.' *J. Anim. Ecol. 9: 319-27.*
- Oosting, H. J. & Billings, W. D. (1943).** 'The red fir forest of the Sierra Nevada: *Abietum magnificae*.' *Ecol. Monogr. 13: 261-74.*
- Park, T., Gregg, E. V. & Lutherman, C. Z. (1941).** 'Studies in population physiology. X. Interspecific competition in populations of granary beetles.' *Physiol. Zool. 14: 395-430.*
- Pearsall, W. H. (1918).** 'The aquatic and marsh vegetations of Esthwaite Water.' *J. Ecol. 6: 53-74.*
- Pearsall, W. H. (1932).** 'Phytoplankton in the English Lakes. II. The composition of the phytoplankton in relation to dissolved substances.' *J. Ecol. 20: 241-62.*
- Percival, E. (1929).** 'A report on the fauna of the estuaries of the River Tamar and the River Lynher.' *J. Mar. Biol. Ass. U.K. 16: 81-108.*
- Percival, E. & Whitehead, H. (1930).** 'Biological survey of the River Wharfe. II. Report on the invertebrate fauna.' *J. Ecol. 18: 286-302.*
- Pirrie, M. E., Bruce, J. R. & Moore, H. B. (1932).** 'A quantitative study of the fauna of the sandy beach at Port Erin.' *J. Mar. Biol. Ass. U.K. 18: 279-96.*
- Pye-finch, K. A. (1937).** 'The fresh and brackish waters of Bardsey Island (North Wales): a chemical and faunistic survey.' *J. Anim. Ecol. 6: 115-37.*
- Pye-finch, K. A. (1943).** 'The intertidal ecology of Bardsey Island, North Wales, with special reference to the recolonization of rock surfaces, and the rock-pool environment.' *J. Anim. Ecol. 12: 82-108.*
- Rankin, J. S. (1937).** 'An ecological study of parasites of some North Carolina salamanders.' *Ecol. Monogr. 7: 171-269.*
- Sassuchin, D. & Tiflow, W. (1933).** 'Endo- und ecto-

- parasiten des Steppenziegels (*Citellus pygmaeus* Pall.) im Süd-Osten RSFSR.' Z. Parasitenk. 5: 437-42.
- Savage, R. E. (1926).** 'The plankton of a herring ground.' Minist. Agric. Fish., Fish. Invest. Ser. 2, 9, No. 1: 1-35.
- Savely, H. E. (1939).** 'Ecological relations of certain animals in dead pine and oak logs.' Ecol. Monogr. 9: 321-85.
- Scheffer, V. B. & Robinson, R. J. (1939).** 'A limnological study of Lake Washington.' Ecol. Monogr. 9: 95-143.
- Stephenson, T. A., Stephenson, A., Tandy, G. & Spender, M. (1931).** 'The structure and ecology of Low Isles and other reefs.' Great Barrier Reef Expedition 1918-29, Sci. Rep. 3, No. 2: 1-112.
- Steven, D. (1938).** 'The shore fauna of Amerdloq Fjord, West Greenland.' J. Anim. Ecol. 7: 53-70.
- Summerhayes, V. S. & Elton, C. S. (1923).** 'Contributions to the ecology of Spitsbergen and Bear Island.' J. Ecol. 11: 214-86.
- Summerhayes, V. S. & Elton, C. S. (1928).** 'Further contributions to the ecology of Spitsbergen.' J. Ecol. 16: 193-268.
- Tansley, A. G. (1939).** 'The British islands and their vegetation.' Cambridge.
- Tansley, A. G. & Adamson, R. S. (1925).** 'Studies of the vegetation of English chalk. III. The chalk grasslands of the Hampshire-Sussex border.' J. Ecol. 13: 177-223.
- Waters, E. G. R. (1929).** 'A list of the Micro-Lepidoptera of the Oxford District.' Proc. Ashmol. Nat. Hist. Soc. for 1928 (Supplement): 1-72.
- Watt, A. S. (1925).** 'On the ecology of the British beechwoods with special reference to their regeneration. Part II. Sections II and III. The development and structure of beech communities on the Sussex Downs (*continued*).' J. Ecol. 13: 27-73.
- Wells, A. L. (1938).** 'Some notes on the plankton of the Thames Estuary.' J. Anim. Ecol. 7: 105-24.