

could be expected to rise periodically (particularly during the spring snow melting) for many years.

It is very likely that the Soviet Union, after some initial reluctance, will eventually adopt the same attitude towards nuclear power stations as was adopted by the United States after the long public enquiry into the accident at Three Mile Island in 1979. As well as ending the propaganda of the almost absolute safety of nuclear power plants and labelling them as 'potentially dangerous', the US government also recommended that new nuclear power plants be located in areas remote from concentrations of population. The official Soviet policy until the Chernobyl disaster did not take the Three Mile Island lesson into consideration. The long term planning continued to locate nuclear energy plants of different types (including the fast breeders) near large cities in order to heat towns centrally with hot water. Voronezh, Gorky, Leningrad and

some other nuclear power stations are being built much nearer to these cities than the Chernobyl station to Kiev. The Chernobyl disaster will affect future plans, and will certainly make a serious impact on the nuclear generating strategy in many other countries as well.

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#### References

- 1 Medvedev, Z.A. (1979) *Nuclear Disaster in the Urals*. W.W. Norton
- 2 Trabalka, J.R., Eyman, L.D., and Auerbach, S.I. (1980) *Science*, 209, 345–353
- 3 Soran, D.M., and Stillman, D.B. (1982) *An Analysis of the Alleged Kyshtym Disaster*, Los Alamos National Laboratory Report LA-9217-MS
- 4 *Die Presse*, March 18, 1959. Vienna
- 5 Gus'kova, A.K. (1967) *Med. Rad.* 11, 53–64
- 6 Burnazyan, A.I. (1975) *At. Energi.* 39, 167–172
- 7 Mednik, I.G., Tikhomirov, F.A., Prokhorov, V.M. and Karaban, P.T. (1981) *Ekologiya*, no. 1, 40–45
- 8 Molchanova, I.V., and Karavaeva, E.N. (1981) *Ekologiya*, no. 5, 86–88
- 9 Molchanova, I.V., Karavaeva, E.N., Chebotina, M.Ya., and Kulikov, N.V. (1982) *Ekologiya*, no. 2, 45–49
- 10 Buyanov, N.I. (1981) *Ekologiya*, no. 3, 66–70
- 11 Nifontova, M.G., and Kulikov, N.V. (1981) *Ekologiya*, no. 6, 94–96
- 12 Kulikov, N.V. (1981) *Ekologiya*, no. 4, 5–11
- 13 Vennikov, V.A. (1975) In *Methodological Aspects of Study of Biosphere* (in Russian), pp. 55–71, Moscow
- 14 Polushkin, K. (1980) *Nauka i Zhizn*, no. 11, 44–52
- 15 Devel, L., Tovedal, H., Bergstrom, U., Appelgren, A., Chyessler, J. and Andersson, L. (1986) *Nature*, 321, 192–193
- 16 Beardsley, T. (1986) *Nature*, 321, 187
- 17 Aleksakhin, R.M., and Naryshkin, M.A. (1977) *Migration of Radionuclides in Forest Biocoenosis* (in Russian), Nauka

Since Darwin accepted the Malthusian population theory to solve the demographic problems he thought to be logically connected with the universal operation of natural selection, the numerical processes in both populations and communities were generally supposed to be governed by competition. For interspecific relations this found expression in the 'competitive exclusion principle'. After it was shown that coexistence rather than exclusion of closely related species is the rule, this principle gradually changed into the 'competitive niche shift principle'. Recently the universality of competition has been increasingly questioned, so that other interspecific relationships (especially predation) are reevaluated as possibly governing many natural population and inter-population processes.

By considering natural selection as the driving force of evolution Darwin created a new problem: to be naturally selected implies a better chance of leaving descendants, and if conditions remain favourable numbers are expected to increase. In his own words: 'Owing to the high geometrical rate of increase of all organic beings, each area is already fully

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## The Present Status of the Competitive Exclusion Principle

Pieter J. den Boer

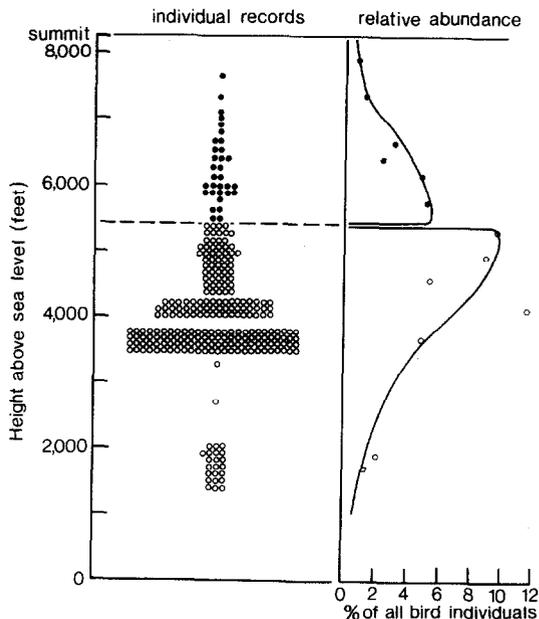
stocked with inhabitants; and it follows from this, that as the favoured forms increase in number, so, generally, will the less favoured decrease and become rare<sup>1</sup>. Darwin thought that this generally occurred by competition, not only between varieties of the same species, but also between species: 'We have reason to believe that species in a state of nature are limited in their ranges by competition of other organic beings quite as much as, or more than, by adaptation to particular climates<sup>1</sup>. Especially closely related species would compete severely: '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<sup>1</sup>.

With this conclusion of Darwin the 'competitive exclusion principle' was born, though it is generally referred to as Gause's principle: 'It is admitted that as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that

each takes possession of certain peculiar kinds of food and modes of life in which it has an advantage over its competitor<sup>2</sup>. The 'niche' of a species is thought to consist of the essential resources of the species inclusive of conditions of time and space as well as the strategy of life which enable it sufficiently to make use of these resources. Therefore, 'competition' is that kind of interaction between individuals of two or more species, by which at least one of the species is kept from sufficiently using its essential resources.

In the 1920s the principle of competition was formalized in the Lotka-Volterra equations. Given the highly restricting assumptions of these models, which state that populations of identical individuals of two species are growing together in a closed and homogeneous environment with constant physico-chemical properties, the principle is tautological: the conclusions are implicit in the assumptions<sup>3</sup>. Laboratory experiments in the 1930s and 1940s, usually with genetically homogeneous stocks of *Tribolium* or *Drosophila* species, aimed at satisfying as closely as possible the premises of the competition equations. They

**Fig. 1.** Two species of *Crateroscelis* warblers on Mt Karimui in New Guinea segregate in their niches by altitude, replacing each other abruptly at 1643 m. Each circle represents one observation of *C. robusta* (filled circles) or *C. murina* (open circles). (Paucity of symbols between 650 and 1050 m is because little time was spent there.) On the right, these observations are re-expressed as the percentage each warbler species contributes to the total number of bird individuals of all species at each altitude. (Based on Ref. 9, with permission of the American Association for the Advancement of Science.)



showed that the logic of the models is indeed irrefutable, but also that the assumptions are so severe that even small deviations from constant or homogeneous conditions might give unpredicted results<sup>4</sup>. Doubts grew about the power of the principle to explain distributional patterns of closely related species living under natural conditions, ending in 1971–72 in a discussion in *Nature* (cited in Ref. 5). The principle mainly survived as the widespread conviction that natural selection should necessarily be 'competitive selection'<sup>6,7</sup>.

During most of this century it has been common to consider that the occupation of separate habitats by closely related species is due to competitive exclusion<sup>8</sup>. Especially intriguing are cases where two con-

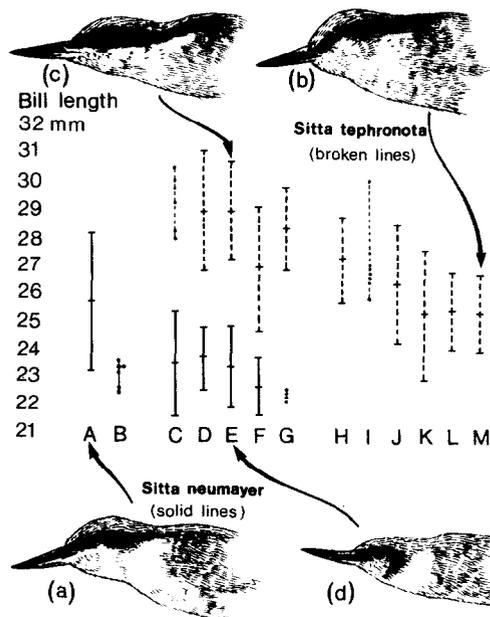
generic species replace each other abruptly over a short distance, e.g. Fig. 1 (Ref. 9). But even observations of this kind (which cannot often be made) are open for other explanations, such as food preferences, requirements for nesting, or highly specific physico-chemical tolerances. The same can be said when the invasion of some species into a new area coincides with, or is followed by, retraction of distribution or at least a striking decrease in numbers of related species<sup>8,9</sup>. Such observations indeed suggest competitive interactions, but other explanations cannot be excluded<sup>10,11</sup>. Where congeneric species are found to coexist it is generally supposed that their niches will differ significantly, either because before meet-

ing the species evolved separately, and thus became adapted to different sets of conditions, or because they coevolved under pressure of competition, and thus diverged in resource utilization<sup>12,13</sup>. The latter phenomenon, which was called 'character divergence' by Darwin, but is better known as 'character displacement'<sup>14</sup>, and is also indicated as 'niche shift'<sup>9</sup> or 'niche segregation', is at present one of the most controversial aspects of community ecology<sup>15</sup>.

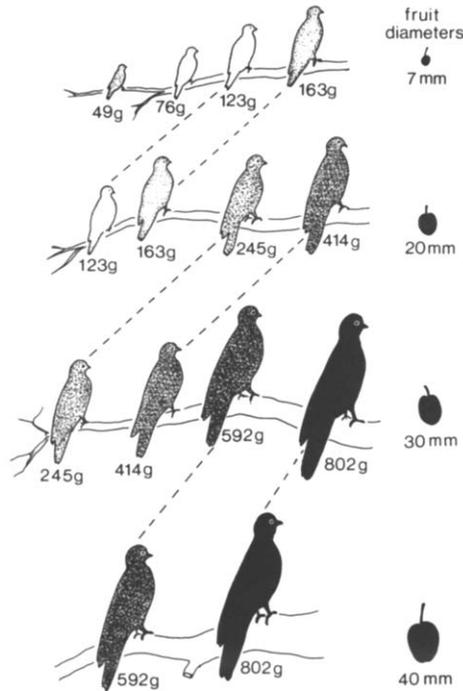
After the war, ecologists had to find their way between axiomatic theorizing and multi-interpretable field observations. As the gap between these poles is wide, and hardly bridgeable, explorations could be undertaken in many different directions. Several authors tried to adapt their conviction of the universality of competition to the growing collection of apparently conflicting field observations, especially those concerning coexistence of supposed competitors: fundamental niche<sup>16</sup>, competition theory<sup>17</sup>, and niche theory<sup>18–21</sup>. Others tried to tackle these questions more directly by performing elegant field experiments<sup>22,23</sup>. Although the possibilities for such experiments are restricted, it has at least been shown that the coexistence of sessile organisms may be significantly favoured by predation, including the feeding of herbivores on plants<sup>22,24</sup>. It was concluded that predation may prevent potential competitors from exceeding the carrying capacity of the environment, and thus will prevent exclusion. The high species richness of certain kinds of vegetation is sometimes attributed to the effects of herbivores<sup>24</sup>.

From the moment of the formulation of the competitive exclusion principle by Gause<sup>2</sup> the danger of circular reasoning has been recognized. However 'similar' closely related species sometimes are, they are different by definition, and so will be their niches. Therefore, to seek ecological differences between coexisting congeneric species proves nothing in itself, because we lack reliable quantitative methods to compare and evaluate the ecological differences and similarities that will naturally (that is, without competitive coevolution) coincide with the morphological differences and similarities between species. We can only show that it is reasonable to suppose that taxonomically closely related species will also be closely related ecologically<sup>5</sup>, but this need not exclude coexistence. The few well-documented cases of direct exclusion under field conditions show

**Fig. 2.** Character displacement in Asiatic nuthatches. Bill length and facial stripe in the two species are very different in areas where they occur together but are quite similar where they occur alone. Populations west of the zone of overlap (*Sitta neumayer*): A, Dalmatia and Greece; B, Asia Minor. In the zone of overlap: C, Azerbaijan and Northern Iran; D, Kermanshah; E, Luristan and Bakhtiari; F, Fars; G, Kirman. East of the zone of overlap (*S. tephronota*): H, Persian Baluchistan; I, southern Afghanistan; J, Khorasan; K, north-central Afghanistan north of the Hindu Kush; L, north-eastern Afghanistan (Pamirs); M, Ferghana and western Tian Shan. (Based on Ref. 30, with permission of McGraw-Hill Book Company.)



**Fig. 3.** Eight species of fruit pigeons *Ptilinopus* and *Ducula* in New Guinea lowland rain forest segregate by size. The number below each pigeon is the average body weight of the species; each species weighs about 50% more than the preceding species. The sketch indicates those pigeon species utilizing fruit of given sizes and the preferred perch position of each species along a branch. Fruit is swallowed whole, and larger pigeons can swallow larger fruits. Smaller pigeons can perch on fine branches and can therefore reach some fruits inaccessible to larger pigeons. But larger pigeons aggressively displace smaller species on branches thick enough to support the heavier species. The pigeons are: 49g, *Ptilinopus nanus*; 76g, *P. pulchellus*; 123g, *P. superbus*; 163g, *P. ornatus*; 245g, *P. perlatus*; 414g, *Ducula rufigaster*; 592g, *D. zoeae*; 802g, *D. pinon*. (Based on Ref. 9, with permission of the American Association for the Advancement of Science.)



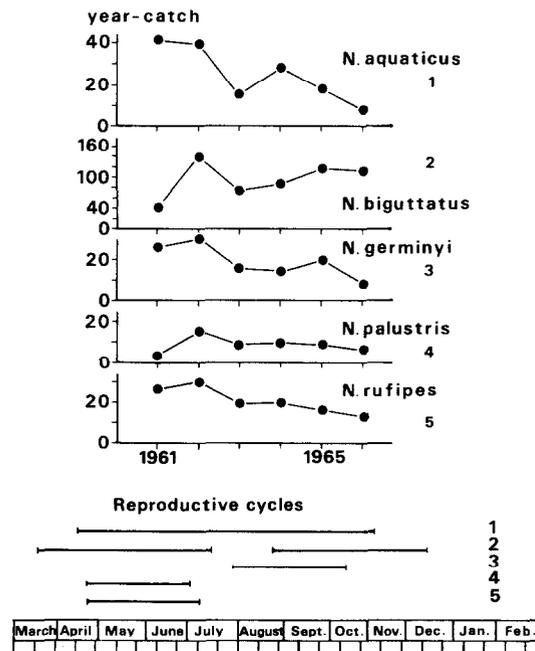
than could be expected with a random distribution of the species<sup>5,7</sup>. The advantages of coexistence of related species are apparently greater than the drawbacks of possible competitive interactions. Obviously, no more is needed also to resolve what is called 'the paradox of the plankton'<sup>29</sup>.

We are left with two hypotheses to explain the coexistence principle: (1) in natural ecosystems, adverse conditions (especially predation *sensu lato*, which is often proportionally more severe at higher densities) are so universal and significant that only very occasionally will the numbers of individuals of the coexisting populations of species with similar resource utilization grow together such that carrying capacity is exceeded, and interspecific competition will rarely become so severe as to result eventually in exclusion of one or more of the species<sup>10</sup>; (2) under favourable conditions the ecological differences between closely related species are generally sufficient to allow coexistence to begin, after which the gradually increasing pressure of competition will shift the niches such

that the excluding species rendered essential resources unavailable for the excluded species<sup>25</sup>, either by direct aggression (ants), or by claiming the entire resource (parasitoids), or (within a closed environment) by more rapidly using up the resource (worms in intestines, insect larvae in fruits, droppings, carrion, etc.)<sup>26</sup>, or through interspecific territoriality (some pomacentrid fish), or (among sedentary animals) by simply pushing away the competitor (barnacles, limpets, anemones)<sup>25</sup>. However, such events will not only occur between related species; for instance, monkeys that remove fruits from a tree will deprive the insects that lay their eggs in those fruits. Hence, the laboratory experiments on exclusion (above) can be considered, at best, as models for species living in closed and comparatively small environments, such as fruits, flower heads, plant galls, or intestines<sup>26</sup>.

In spite of the above remarks, if closely related species in the field have a higher chance of excluding one another than less related species, it must be possible to test the hypothesis that 'species belonging to different genera will more frequently coexist than congeneric species', against the appropriate null hypothesis. This was first appreciated and applied to flowering plants, insects and birds by Williams<sup>27</sup>, followed by Simberloff<sup>28</sup> for vascular plants, ants and birds on islands, and by den Boer for carabid beetles<sup>5</sup>. These tests led to the conclusion that congeneric species coexist more frequently than could be expected from a random distribution of species over habitats (or islands), so that the 'exclusion principle' could be re-

placed by the 'coexistence principle': 'As taxonomically closely related species usually are also ecologically closely related, related species will be found coexisting more frequently



**Fig. 4.** During the six years of observation populations of five species of small ground beetles of the genus *Notiophilus* were found to occupy the same small birch wood (about 800 square meters), in Drenthe, The Netherlands. Individuals of all species are of the same size (about 5 mm) and have the same feeding habits: adults as well as larvae are surface dwelling hunters of Collembolus. Adults locate springtails by eye, the larvae by tactile stimuli. Year-catches resulted from continuous pitfall sampling in the centre of the wood, and were equivalent to 0.1–1% of population size. Four of the five species reproduce in spring, and three also (or exclusively) in autumn. These data show that five of the six *Notiophilus* species in the area are able to coexist, though they occupy virtually the same niche; only *N. substriatus* was absent from this simply structured wood, which consists of birches of about the same age. The species of this genus, which are identified with the help of small, but distinct, structural differences, such as elytral intervals, microsculpture, form and punctuation of the pronotum, frontal furrows (see photographs), are identical in 'hunting morphology': mandibles, size and field of vision of the eyes, long slender legs. (Data of the Biological Station, Wijster, The Netherlands (Refs 5, 7); scanning photographs TFDL, Wageningen.)

that this early coexistence can be continued<sup>9</sup>. The latter hypothesis predicts that the ecological differences between sympatric populations of the supposed competitors will have become greater than between primarily allopatric populations.

Though the second hypothesis, which replaces the 'competitive exclusion principle' by the 'competitive niche shift principle', seems to be more favoured by ecologists than the former<sup>12,18</sup>, it now meets with a growing resistance<sup>15</sup>. In the context of competition theory it was undoubtedly a step forward to compare sympatric populations of two potential competitors with allopatric ones<sup>14</sup>. The difficulty was, however, that most ecological phenomena can only be quantified by many years of intensive field work, so that for quick inference one had to manage with measurable morphological characters that could be supposed to be directly related to the manner and degree of resource utilization, such as body sizes and bill dimensions in birds. The example of bill lengths in two Asiatic nuthatches (*Sitta*) seemed to be so convincing that it was used in text books<sup>8,30</sup> (Fig. 2). It can be shown, however, that this classical case of 'character displacement' simply represents two parallel character clines without indications of niche shift between the sympatric populations<sup>31</sup>. Note that if the clines M-C and G-A in Fig. 2 had not run from right below to left above, but from right above to left below, nobody would ever have suggested, when comparing the situation at E with those at M and A, the occurrence of niche shift with connected character displacement. Though not all cases of character displacement<sup>14</sup> can be invalidated as easily as this, it is increasingly clear that character displacement is not a promising field of research<sup>7,32-34</sup>.

If the niche segregation necessary for permanent coexistence had occurred so long ago that the character distance had become a general feature of the species concerned, we can no longer observe any character displacement. It then becomes a question of taste whether one assumes that the ecological differentiation of presently coexisting species originated from competitive coevolution in the past, or from separate evolution under different conditions<sup>13</sup>. In fact, by referring to competition past the problem has been manoeuvred outside the field of science. Whether examples of present niche segregation by size, such as pictured in Fig. 3, are the outcome

of past interspecific competition (possibly maintained by intolerant behaviour) will have to stay undecided. The message of Fig. 3 seems to be: if they are to avoid severe interspecific competition, no more than two coexisting species of these fruit pigeons can have exactly the same feeding habits, and in that case they will differ appreciably in size<sup>9</sup>. But such specialization need not be associated with competition, as is clearly illustrated by phytophagous insects<sup>36</sup>. Moreover, it is not difficult to find examples of coexisting congeneric species of the same size and feeding habits (Fig. 4). We cannot, however, make science by selecting examples. We will have to judge the actual frequencies of these examples in their natural context, and to test against the correct null hypothesis<sup>7,37</sup>. A thorough frequency analysis of different kinds of coexistence could indeed give valuable hints about probable and less probable evolutionary processes<sup>15</sup>.

As a future trend we can expect a further depreciation of competition, both intra- and interspecific, as being a major force in ecology and evolution. The manifold influences of weather, climate and other physical factors<sup>38</sup> will assume greater importance, and the claim of universality of competition will probably be replaced by a gradual reevaluation of the role of predation<sup>10,13,24,32,35</sup>. The first hypothesis (above) to explain the coexistence of related species will enter a period of extensive testing.

#### References

- Darwin, C. (1878) *The Origin of Species*, (6th ed.), John Murray
- Gause, G.F. (1934) *The Struggle for Existence*, Williams & Wilkins
- Peters, R.H. (1976) *Am. Nat.* 110, 1-12
- Ayala, F.J. (1970) in *Essays in Evolution and Genetics in Honour of Theodosius Dobzhansky*, (Hecht, M.K. and Steere, W.C., eds), pp. 121-158, North Holland
- Den Boer, P.J. (1980) *Neth. J. Zool.* 30, 278-306
- Nicholson, A.J. (1960) in *Evolution after Darwin* (Tax, S., ed.), pp. 477-521, Chicago University Press
- Den Boer, P.J. (1985) *Z. Zool. Syst. Evolutionforsch.* 23, 259-274
- Mayr, E. (1963) *Animal Species and Evolution*, Belknap Press, Harvard University
- Diamond, J.M. (1978) *Am. Sci.* 66, 322-331
- Andrewartha, H.G. and Birch, L.C. (1954) *The Distribution and Abundance of Animals*, Chicago University Press
- Lack, D. (1971) *Ecological Isolation in Birds*, Blackwell
- Cody, M.L. and Diamond, J.M., eds (1975) *Ecology and Evolution of Communities*, Belknap Press
- Connell, J.H. (1980) *Oikos* 35, 131-138
- Brown, W.L. and Wilson, E.O. (1956) *Syst. Zool.* 5, 49-64
- Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., eds (1984) *Ecological Communities. Conceptual Issues and the Evidence*, Princeton University Press
- Hutchinson, G.E. (1958) *Cold Spring Harbor Symp. Quant. Biol.* 22, 415-427
- MacArthur, R.H. (1972) *Geographical Ecology*, Harper & Row
- Pianka, E.R. (1976) in *Theoretical Ecology*, (May, R.M., ed.), pp. 167-196, Blackwell
- Cody, M.L. (1975) in *Ecology and Evolution of Communities* (Cody, M.L. and Diamond, J.M., eds), pp. 214-257, Belknap Press
- Diamond, J.M. (1975) in *Ecology and Evolution of Communities* (Cody, M.L. and Diamond, J.M., eds), pp. 342-444, Belknap Press
- Hutchinson, G.E. (1975) in *Ecology and Evolution of Communities* (Cody, M.L. and Diamond, J.M., eds), pp. 492-521, Belknap Press
- Connell, J.H. (1975) in *Ecology and Evolution of Communities* (Cody, M.L. and Diamond, J.M., eds), pp. 460-490, Belknap Press
- Wise, D.H. (1984) in *Ecological Communities. Conceptual Issues and the Evidence* (Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., eds), pp. 42-53, Princeton University Press
- Huffaker, C.B. (1971) in *Dynamics of Populations* (Den Boer, P.J. and Gradwell, G.R., eds), pp. 327-343, PUDOC
- Birch, L.C. (1979) *Fortschr. Zool.* 25, 197-221
- Zwölfer, H. (1979) *Fortschr. Zool.* 25, 331-353
- Williams, C.B. (1964) *Patterns in the Balance of Nature*, Academic Press
- Simberloff, D.S. (1970) *Evolution* 24, 22-47
- Ghilarov, A.M. (1984) *Oikos* 43, 46-52
- Ehrlich, P.R. and Holm, R.W. (1963) *The Process of Evolution*, McGraw-Hill
- Grant, P.R. (1975) in *Evolutionary Biology* (Dobzhansky, T., Hecht, M.K. and Steere, W.C., eds), Vol. 8, pp. 237-337, Plenum Press
- Strong, D.R. (1983) *Am. Nat.* 122, 636-660
- Hairton, N.G. (1984) in *Ecological Communities. Conceptual Issues and the Evidence* (Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., eds), pp. 19-27, Princeton University Press
- Simberloff, D.S. (1984) in *Ecological Communities. Conceptual Issues and the Evidence* (Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., eds), pp. 234-253, Princeton University Press
- Strong, D.R. (1984) in *Ecological Communities. Conceptual Issues and the Evidence* (Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., eds), pp. 28-41, Princeton University Press
- Jermy, T. (1985) *Z. Zool. Syst. Evolutionforsch.* 23, 275-285
- Strong, D.R. (1980) *Synthese* 43, 271-285
- Andrewartha, H.G. and Birch, L.C. (1984) *The Web of Ecology. More on the Distribution and Abundance of Animals*, Chicago University Press