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Holism and reductionism in biology and ecology

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CHAPTER 13

THE INHIBITORY EFFECT OF THE HOLISM-REDUCTIONISM DISPUTE: A CONTROVERSY IN ISLAND BIOGEOGRAPHY AND ITS SOLUTION⁹⁶

13.1 Introduction

In this final chapter I will discuss an example of the inhibitory effect which the holism-reductionism dispute may have on the growth of knowledge. The example concerns a controversy in island biogeography between two of the research programmes involved in the concretizations of the MacArthur-Wilson model discussed in the previous chapter. The one programme, led by Jared Diamond, is moderately reductionistic but also has some radically holistic features. It assumes that communities are integrated wholes whose structure is determined primarily by *interspecific competition*. The other programme, led by Daniel Simberloff, is radically reductionistic. It claims that the so-called 'structure' of communities can be explained fully in terms of *random colonization*, given some properties of species and islands.

The controversy was induced by a paper by Diamond (1975a) in which he argues that communities are stable, integrated entities whose structure results from strictly deterministic 'assembly rules'. The main factor underlying these rules, according to Diamond, is interspecific competition. His paper was heavily criticized by Simberloff (1978) and Connor and Simberloff (1979), who reject the whole idea of assembly rules and also question the importance of competition. They argue that one should always first test the 'null hypothesis' that the so-called structure of communities is completely random before turning to alternative, biological explanations.

The controversy has lasted about ten years (a long period of time, considering the age of ecology), appears to have bled to death rather than to have been settled⁹⁷, and has produced nothing new in the field of descriptions and explanations of community structure. Since it is fed by conflicting, *in casu* holistic and reductionistic views of communities, it forms a good example of the inhibitory effect which holism-reductionism disputes may have on the growth of knowledge (Hagen 1989; see 8.3.3).

This raises a problem, however, for my claim that in ecology, too, holism and reductionism should be seen as mutually dependent and co-operating research programmes rather than as conflicting views of nature. For controversies like this one (and it is not the only one) rather seem to point to the opposite. The problem can be solved, however, by showing that eventually the controversy can, and in a sense has been, resolved in a way that corroborates my claim. In order to do so, I will enter in considerable detail into the nature of the controversy and into the factors that have played a role in its origination as well as its

⁹⁶The basis for this chapter was laid by Ernst Oosterveld (1985) who first analysed the controversy and brought it to my attention. Later, I have had many stimulating discussions about it with both Ernst and Henny van der Windt (Looijen et al. 1993). I owe many of the ingredients for this chapter to Ernst and Henny. However, the current presentation of the controversy, and of its solution, is mine.

⁹⁷According to Lewin (1984) the conflict is so serious that it "has split the discipline in two so decisively that for some individuals reconciliation is an unlikely prospect". I will show that we need not be so dramatic.

duration. In particular, I will enter extensively into Diamond's (1975a) original paper, because a good insight into this paper will prove to be of crucial importance in resolving the controversy.

13.2 The competition programme

13.2.1 The structure of communities

Underlying the controversy is one of the most intriguing but also toughest and controversial issues in ecology, namely the question of how to explain differences in the structure of communities. Why are there more and/or other species in the one community than in the other?

A major school of ecologists is of the opinion that the answer to this question is to be found in the trophic relations of species, particularly interspecific competition. A great number of hypotheses, principles and models have been developed by this school, which go together under the names of niche theory and competition theory (see chapter 11). The core principle of this theory is the competitive exclusion principle: if two or more species have identical niches they cannot coexist in the same community (but see chapter 11). With this principle one can explain the coexistence (or displacement) of species and, hence, the structure (species number and composition) of communities. Since especially Robert MacArthur has done much work in extending the theory, this school is often referred to as the MacArthur school.

Diamond is a typical representative of the MacArthur school. Though originally a membrane physiologist, he is also a respected ecologist and biogeographer. In a voluminous paper entitled "Assembly of species communities" (Diamond 1975a), he argues that ecological communities are stable, integrated entities whose structure is brought about by strictly deterministic '*assembly rules*'. With 'stable' Diamond means that the species composition of communities will persist with little change if there is no change in the physical environment, and that the component species are able to *resist invasion* by new species.⁹⁸ This resistance against invasions is expressed by the assembly rules. These are constraints determining which combinations of species can occur in a community and which combinations can't. According to Diamond, the major integrating factor underlying these rules is *interspecific competition*. His 'working hypothesis' states that "through diffuse competition [that is, competition between several species], the component species of a community are selected, and coadapted in their niches and abundances, so as to fit with each other and to resist invasion" (Diamond 1975a, p. 343).

13.2.2 Incidence functions

In order to test his hypothesis, Diamond investigated land bird communities on islands of the Bismarck archipelago near New Guinea. This archipelago consists of approximately 50 islands where (at the time) a total number of 141 species of non-marine breeding birds occurred. The area of the islands varies from less than 0.1 km² to several thousand km². The number of species per island varies from 3 to 127. Diamond obtained complete lists of which species

⁹⁸This is somewhat surprising because especially Diamond has done a lot of research on the turnover of species on islands. See chapter 12.

occurred on which islands.

To quantify how non-randomly the species are distributed on the islands, Diamond construed so-called 'incidence functions', which relate for each species its probability of occurring on an island to the total number of species on that island. Diamond grouped the islands into classes sharing a similar total number of species (0-3, 4-6, 7-10, 11-20, etcetera) and calculated for each species its incidence of occurrence, J , on islands in a given class. This incidence of occurrence is the fraction of islands in a given class on which the species occurs (varying from 0, when the species occurs on none of the islands in that class, to 1, when it occurs on all islands in that class). He then plotted for each species its incidence of occurrence in each class against the average total number of species in each class, S . A species' incidence function, $J(S)$, is the line connecting the various points thus obtained (figure 13).

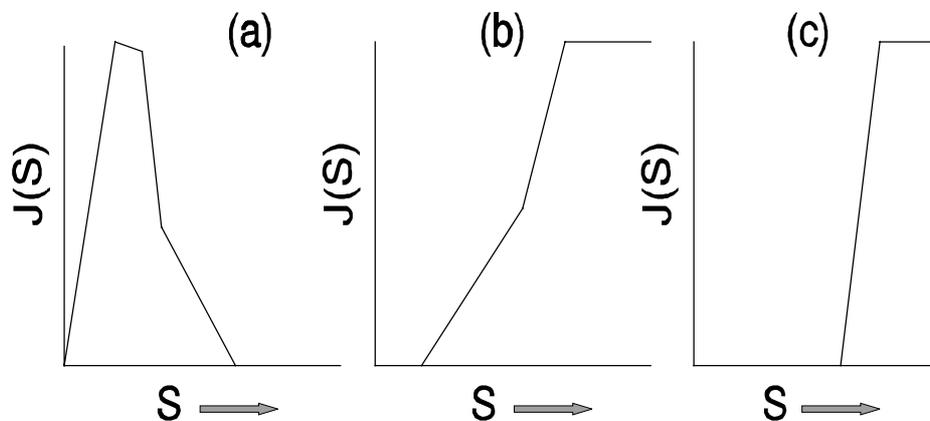


Figure 13: Typical shape of incidence functions of a supertramp (a), a tramp (b) and a high-S species (c) (after Diamond 1975).

On the basis of these incidence functions Diamond distinguishes three groups of species: (1) a group of 52 so-called 'high-S' species, which are exclusively confined to the most species-rich islands ($S > 81$); (2) a group of 13 so-called 'supertramps', which are exclusively confined to islands with low numbers of species ($S < 16$); and (3) a group of 'tramps', which occur mostly on species-rich islands but to a lesser extent also on species-poor islands.⁹⁹

It is important to note that, according to Diamond, the form of the incidence functions depends largely on the properties of each species, such as its dispersal ability, biotope¹⁰⁰ preference, minimum territory requirement, resource requirements and size of population

⁹⁹Within the group of tramps, Diamond makes a further distinction between A-, B-, C- and D-tramps, but this is of no particular interest to this chapter.

¹⁰⁰As so many, Diamond uses the term 'habitat' instead of 'biotope'.

fluctuations, and on island characteristics meeting these abilities, preferences and requirements. There is a strong influence of island area: larger islands generally contain more biotopes, larger food supplies, and they sooner meet the minimum territory requirements of species. Smaller islands are often also more isolated islands, moreover, and hence less easy to reach for species with low dispersal abilities. In addition, every species has a certain chance of becoming locally extinct due to stochastic fluctuations in the number of births and deaths, and this chance is the higher the smaller an island (see chapter 12). Therefore, according to Diamond, the incidence functions are largely a reflection of the species-area relation: the islands vary strongly in area and the larger an island, the higher the number of species it contains. This means that the S-classes may actually be regarded as area-classes and that the incidence functions largely reflect the fact that the chance of finding a species on an island increases with island area.

However, if area were the sole determinant of a species' incidence of occurrence, one would expect each species to have roughly the same incidence function, namely a monotonously increasing line from the origin to the maximum value of 1. For the average chance of a species occurring on an island would then be equal to the total number of species on an island (being determined by island area) divided by the total number of species in the archipelago. This chance is almost 0 on the smallest islands containing only a few species, and increases to almost 1 on the largest islands containing almost all species of the archipelago. This pattern holds *grosso modo* for the incidence functions of the tramps and to a large extent also for the incidence functions of high-S species, but there are two large deviations: (1) the total absence of high-S species on small islands; and (2) the total absence of supertramps on large islands.

The former deviation is explained by Diamond through the fact that many high-S species are confined to rare biotopes (fresh water, marsh, grassland, and high mountains) which occur only on the larger islands. Other high-S species require a large feeding territory which they find only on large islands. In addition, many high-S species have relatively low dispersal abilities and are unable, therefore, to reach the smaller, more isolated islands. Finally, high-S species generally have low reproductive rates and are therefore particularly apt at becoming extinct on small islands.

The latter two factors allow Diamond at the same time to explain why supertramps do occur especially on small islands. All supertramp species are good dispersers and although they too face the chance of becoming extinct on small islands, they are able to recolonize them faster and more frequently than other (high-S) species. Moreover, supertramps have high reproductive rates and therefore are able to spread so fast and become so abundant by the time that other species arrive that there is simply no place left for the latter.

The only thing that Diamond cannot explain in terms of properties of species and island characteristics is the complete absence of supertramps on large, species rich islands. Supertramps are easily capable of reaching all islands in the archipelago, and all islands contain suitable biotopes. The explanation can neither be found in predation or competitive exclusion by other species than birds, because both predators and competitors in the form of mammals and reptiles are at least as abundant on small islands as they are on large islands. According to Diamond, the explanation must be competitive exclusion by other bird species.

13.2.3 Assembly rules

Diamond formulates the same problem - the absence of supertramps on large islands - in

another way by noting that the properties of individual species and islands are insufficient to explain the specific *composition* of the bird communities on the islands. According to him, it is more exclusive than one would expect on the grounds of the species' incidence functions alone: on every island only certain combinations of species occur while others, which could occur if one looks at the incidence functions of the relevant species, don't. Diamond points in particular to so-called checkerboard patterns in the distributions of two species (of which in each case one is a supertramp), where each island contains either the one species or the other, but never both (and sometimes neither of them). He notes that each of these cases pertains to ecologically closely related species which exploit the same resources and have similar resource exploitation strategies. According to Diamond, these species cannot co-occur on an island: the one (the supertramp) is competitively excluded by the other.

Diamond faces the problem, however, that there are also islands containing neither of the species in such an exclusive species pair, so that the distribution of the one species cannot be fully explained in terms of competitive exclusion by the other. He solves this problem by noting that these islands do contain other combinations of ecologically related species. Such groups of ecologically related species are called *guilds* (Root 1967). In order to show the importance of competition, Diamond restricts his further analysis to four such guilds.

He calculates for all possible combinations of species in a guild the chance of a combination occurring on an island in a given S-class by multiplying the individual chances of the species of that combination occurring on an island in that S-class. These individual chances follow from the species' incidence functions. Next he determines all existing combinations of species on the islands and he compares for each combination its frequency of occurrence on islands in a given S-class with the expected chance of its occurrence on islands in that class. It appears then that some combinations occur less often than expected and this fact is recorded by Diamond in the form of seven rules, or constraints, which according to him govern the assembly of communities.¹⁰¹ These 'assembly rules' are:

- A. If one considers all the combinations that can be formed from a group of related species, only certain ones of these combinations exist in nature.
- B. Permissible combinations resist invaders that would transform them into forbidden combinations.
- C. A combination that is stable on a large or species-rich island may be unstable on a small or species-poor island.
- D. On a small or species-poor island, a combination may resist invaders that would be incorporated on a larger or more species-rich island.
- E. Some pairs of species never coexist, either by themselves or as a part of a larger combination.
- F. Some pairs of species that form an unstable combination by themselves, may form part of a larger stable combination.
- G. Conversely, some combinations that are composed entirely of stable sub-combinations are themselves unstable.

¹⁰¹Diamond starts by formulating so-called incidence rules, compatibility rules and combination rules, and he unites these rules in his assembly rules. The distinctions are of no further importance.

13.2.4 Diffuse competition

According to Diamond, combinations that do not occur (and these are always combinations with a supertramp) are combinations of species that competitively exclude each other. This forces him, however, to appeal to the rather vague concept of 'diffuse competition', that is, competition between several species. Diamond himself admits the weakness of this concept: "The power of this concept is that, in principle, it can explain anything. Its heuristic weakness is that, if it is important at all, its operation is likely to be so complicated that its existence becomes difficult to establish and impossible to refute" (Diamond 1975a, p. 348). This is indeed the problem. It is difficult enough to prove the competitive exclusion of one species by another, let alone the exclusion of one species by a combination of others. The mechanism that Diamond assumes is that combinations of high-S species on large islands reduce the existing resources to levels which allow themselves to maintain stable populations but which are too low for supertramps. To be able to show this, one needs to have data on both the production of resources and their consumption by each species, as well as knowledge of each species' minimum resource requirements. Diamond has data only of each species' diet.

Diamond does provide some arguments that lend his theory some plausibility. One of these arguments is based on the theory of r - and K -selection (see 11.3.5). According to Diamond, supertramps represent the extreme of r -selected species, that is, species with a high reproductive rate (r , a population's intrinsic growth rate). These are often species of instable biotopes, which keep their population size well below the carrying capacity of the biotope, reproduce themselves quickly and disperse easily. This investment in reproduction and dispersal comes at the expense, however, of efficiency of resource use and hence competitive ability. r -Selected species are mostly generalists, with a broad biotope preference and food choice. So are supertramps: they have high reproductive potential, breed fast, disperse widely, squander resources and thereby tolerate anything and specialize in nothing. High-S species, on the other hand, are K -selected food specialists. K -selected species are mostly species of relatively stable biotopes, which keep their population size at or near the carrying capacity (K) of the biotope and invest more in harvesting efficiency than in reproduction and dispersal. Therefore, according to Diamond, each of the high-S species in a combination is more efficient in exploiting some fraction of the resources, which a supertramp could potentially exploit, than this supertramp itself, so that the latter would have no chance of settling or maintaining itself in their midst.

This explanation sounds plausible and Diamond is able to make it more plausible by dismissing alternatives (predation, competitive exclusion by non-bird species, and chance). In addition, he points to changes in the incidence functions of species as a function (supposedly) of the number of competitors in an archipelago: some species that are supertramps in the Bismarck archipelago, where they meet many competitors, are tramps (that is, occur also on large or species-rich islands) in the Solomon archipelago and on the New Hebrides, where far less competitors occur (see also Diamond 1982). This, too, lends some credibility to his theory, but constitutes no proof.

A final argument provided by Diamond in favour of his theory is that there are shifts in the niches of supertramps as a (supposed) result of the presence of competitors. In my view, however, this is a somewhat unfortunate argument, because though niche-shifts may be seen as indications of competition, they rather have the effect of reducing the intensity of competition and allowing species to coexist instead of one of them being excluded.

13.3 The 'null' programme

13.3.1 The ghost of competition past and naive falsificationism

Shortly summarizing, Diamond concluded from patterns in the distribution of species that these patterns were caused by competition, without, however, producing independent evidence for this theory. For this reason, his paper has been heavily criticized by Daniel Simberloff and his colleagues (Simberloff 1978; Connor & Simberloff 1979; Strong et al. 1979). These critics reject the appeal to what Connell (1980) aptly called 'the ghost of competition past' (current patterns would have been caused by competition in the past). They also criticize Diamond's assembly rules.

The strategy of these critics is remarkable. They notice that "although many imaginative theories have been invented to propose how competition could structure multi-species nature, such theories have rarely been treated as alternative hypotheses and, thus, have not been tested critically. Instead, research is often directed at finding particular circumstances that are consistent with competition theory, while ignoring contradictory evidence. (...) This trend, of course, is counter to the traditions of modern science, which has made much progress by attempting to disprove universal hypotheses such as competition" (Strong et al. 1979, p. 909). They argue that competition theory has rarely if ever been critically tested against the 'null hypothesis' that community structure is apparently 'random', by which they mean: is the result of stochastic colonization, given the properties of individual species and islands. According to Simberloff c.s., one must always first test this null hypothesis before turning to deterministic forces such as competition. They justify this strategy by appealing to Popper's naive falsificationism: "As Popper (1963) points out, it is easy to find confirmatory evidence for most reasonable hypotheses, but science progresses by a different route: by posing testable hypotheses and then attempting to falsify them" (Connor & Simberloff 1979, p. 1138).

The anti-competitionists, as they have come to be called, also claim that their null hypothesis is the simplest hypothesis, because it assumes no deterministic biological forces, and therefore is logically favourite over other hypotheses: "However, we propose another possibility with *logical primacy* over other hypotheses, that other hypotheses must be tested against (...). This is the null hypothesis that community characteristics are apparently random" (Strong et al. 1979, p. 910)

13.3.2 The null hypothesis: random matrices

Simberloff (1978) starts by raising some moderate objections against Diamond (1975a). He notes that the method Diamond used to construct his assembly rules fails in at least two respects. Firstly, Diamond provides no confidence limits so that one cannot assess the significance of failure of a particular species' combination to exist on an island. Secondly, there are probably so few islands in each S-class that the non-existence of certain species pairs on some islands need not be surprising at all, a problem which is exacerbated for combinations of many species. "In sum, until an avifauna is actually assembled by these rules, one is left with the uneasy feeling that the rules lack predictive power, in that all the data are required before any prediction can be made" (Simberloff 1978, p. 723). In short, argues Simberloff, we should first test whether the species are not distributed randomly on the islands before concluding to such deterministic forces as competition.

He performs such a test with one of his colleagues, Edward Connor (Connor & Simberloff 1979). Connor and Simberloff's (1979) critique on Diamond (1975a) becomes much more fierce. They argue that three of Diamond's assembly rules are tautologies, that one cannot be tested, and that the remaining three are in perfect agreement with the null hypothesis that the species composition on islands is the result of random colonization.

Since Connor and Simberloff had no access to the Bismarck data set (which has never been published), they used data on bird species in the New Hebrides and on bird and bat species in the West Indies. They perform computer simulations of random colonization of the islands by species. Their procedure consists of the construction of presence/absence matrices, where the matrix rows represent species and the matrix columns represent islands, and where the elements 0 and 1 stand for the absence and presence, respectively, of a species on an island. According to the Monte Carlo procedure (random drawing with replacement), they randomly draw species from the species pool and place them on randomly chosen islands until the matrix is 'full'. The point where the matrix is considered full is determined by three constraints: (1) the number of species per island (the marginal sum of rows) is constant for each island and equal to the empirical number in the data set; (2) the number of islands per species (the marginal sum of columns) is constant for each species and equal to the empirical number; and (3) the fraction of islands with a particular number of species (that is, islands in a particular S-class) on which a species occurs, is constant for each species and equal to the empirical number. The third constraint means that Diamond's incidence functions are maintained.

These constraints serve to make the null hypothesis biologically realistic: it would be biologically absurd not to take account of differences in species richness between islands as a result of differences in area, and of differences between species in dispersal and colonization abilities.

Connor and Simberloff repeat their procedure ten times for each data set, and then they count in each matrix the number of pairs and trios of species occurring on 0 islands, 1 island, 2 islands, etcetera. They use X^2 -tests to compare the simulated values with the empirical values.

In the case of the New Hebrides birds there appear to be no significant differences between the simulated and the empirical values, and thus there is no reason to reject the null hypothesis. Things are different, however, for the birds and bats in the West Indies. In both cases the empirical values deviate significantly from the simulated values. Nevertheless, and amazingly in view of their purported falsificationism, Connor and Simberloff do not reject the null hypothesis. Instead they claim that there would also be many exclusive species pairs and trios had the species been distributed randomly, subject only to the above constraints. With this 'result' they attack Diamond's assembly rules.

As a matter of fact, they note, three of these rules, rules A, E and G, say nothing more than that only some of all possible combinations of species actually occur in nature. According to Connor and Simberloff, this is in full agreement with their null hypothesis. Since there are innumerable many possible combinations, the chances of some combinations not actually being found on some islands are high. In no way does it follow that these combinations are 'forbidden' by competition.

13.3.3 Tautologies

Things are even worse with the other rules. According to Connor and Simberloff, rule F is untestable and rules B, C and D are tautologies. Rule B, for example, states that "Permissible combinations resist invaders that would transform them into forbidden combinations". Diamond defines a permissible combination as combination that exists and a forbidden combination as a combination that doesn't exist. He further believes that interspecific competition is the deterministic explanation for these existing or non-existing combinations. It follows that he believes that permissible combinations actively resist their transformation into forbidden combinations. According to Connor and Simberloff, however, it follows from their test that the distributional patterns in themselves require no explanation in terms of active resistance "unless one *begins* with the assumption that a distributional gap must be explained by active resistance, in which case we have a tautology and why bother with the exercise of producing evidence?" (Connor & Simberloff 1979, p. 1136).

The same applies to rule C: "A combination that is stable on a large or species-rich island may be unstable on a small or species-poor island". Since Diamond uses the number of species as an operational definition of island area, the words 'large' and 'small' may be left out. Furthermore, the terms 'stable' and 'unstable' are nowhere defined. They are probably used as synonyms for 'permissible' and 'forbidden', respectively, and these terms are, if one doesn't start from the assumption of competitive exclusion, synonymous for 'existing' and 'non-existing'. So rule C becomes: "A combination which is found on species-rich islands may not be found on species-poor islands". However, every species-rich island will contain far more combinations of species than a species-poor island. Thus, according to Connor and Simberloff, rule C is a trivial consequence of the definitions of 'rich' and 'poor' and the most elementary laws of arithmetics.

With respect to rule D, "On a small or species-poor island, a combination may resist invaders that would be incorporated on a large or species-rich island", Connor and Simberloff note that it seems to be a combination of rules B and C and therefore both a tautology (since active resistance must be assumed if active resistance is to be proved) and a direct consequence of the definitions of 'rich' and 'poor'.

Rule F, finally, "Some pairs of species that form an unstable combination by themselves, may form part of a larger stable combination", is untestable in the view of Connor and Simberloff, because there are no islands in the Bismarck archipelago, the New Hebrides or the West Indies that contain only two species, while there is only one island in the Bismarck archipelago containing three species. Hence, there is no way of knowing whether there are two species, A and B, that would form an unstable pair when occurring together with no other species. Whenever A and B co-occur, they do so in combination with one or more other species C. By its mere existence, the resulting larger combination, ABC, will be defined as stable. So rule F boils down to: "Some pairs of species which are not found alone (..) *are* found together with other species". Or should it be: "Every pair of species which is found at all is found with other species". To which Connor and Simberloff add sarcastically: "and what has this to do with competition?" (Connor & Simberloff 1979, p. 1138).

Connor and Simberloff end up by stating that "all this is not to say that species *are* randomly distributed on islands, or that interspecific competition does not occur. Rather, statistical tests of properly posed null hypotheses will not easily detect such competition, since it must be embedded in a mass of not-competitively produced distributional data" (Connor &

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Simberloff 1979, p. 1138). In order to prove competitive exclusion, they assert, one needs observations of active replacement of one species by another, experiment, or very detailed autecological study.

13.4 Reply

13.4.1 Obsolete philosophy

Of course, a reply could not stay out. In two papers written with a colleague, Michael Gilpin, Diamond counter-attacks his critics. Diamond and Gilpin (1982) criticize Connor and Simberloff's null model. Gilpin and Diamond (1982) formulate an alternative, and in their view better, null model in order once more to show the importance of interspecific competition. They get support from other ecologists.

To start with, Diamond and Gilpin do not at all agree with the claims of Simberloff c.s that their null hypothesis is the most parsimonious hypothesis and has logical primacy over other hypotheses: "we disagree with these dogmas, and (..) we view the parsimonious null hypothesis of Connor and Simberloff as nothing more than one of many possible competing hypotheses, one that is implausible, unparsimonious, and definitely not null with respect to competition" (Diamond & Gilpin 1982, p. 64; see also Grant & Abbott 1980; Wright & Biehl 1982; Harvey et al. 1983; Quinn & Dunham 1983; Roughgarden 1983).

Popperian falsificationism is also fired at, as it "represents a particular view of science stemming from the logical positivism of the 1920's [..which..] took it on faith that philosophy could prescribe rather than describe how science proceeded, and that certain formal procedures (such as construction of null hypotheses) could be specified as essential for success in science as in logic. Many philosophers today consider this faith a delusion, make little reference to progress by falsification, and have pluralistic views of how science operates" (Diamond & Gilpin 1982, p. 74).

It may be noted at the outset that this criticism is partially accepted by Simberloff: "I even agree with Roughgarden and with Quinn and Dunham that we were incorrect to suggest (Strong et al. 1979) that the hypothesis of no population interactions has "logical primacy" as a null hypothesis" (Simberloff 1983, p. 629; see also Connor & Simberloff 1983, 1986). Meanwhile, he has also been converted to Lakatos' refined falsificationism (see Simberloff 1983).

13.4.2 Restriction to guilds

Diamond and Gilpin (1982) point to a number of 'flaws' in the procedure of Connor and Simberloff. The most important one is that their analysis was performed using entire species sets, whereas it should have been restricted to guilds. It is senseless to search for effects of competition in all pairwise interactions between species in an avifauna, because competition can be expected to occur only between members of the same guild, that is, between ecologically related species utilizing the same resources. It is senseless, for instance, to compare owls with hummingbirds, or ducks with warblers. If one does so, he buries distributions influenced by competition in an overwhelming mass of irrelevant data (Diamond & Gilpin 1982, p. 66; see also Grant & Abbott 1980; Alatalo 1982; Bowers & Brown 1982; Wright & Biehl 1982; Harvey et al. 1983; Quinn & Dunham 1983; May 1984). Notice that Connor and Simberloff said exactly the same thing, though with a different intention (see the

last quote in 13.3.3; see also Connor & Simberloff 1983, p. 457).

13.4.3 Hidden structure

A second flaw, according to Diamond and Gilpin, is hidden in the constraints which Connor and Simberloff used. Both the number of species per island (constraint 1) and the number of islands per species (constraint 2) and the incidence functions of species (constraint 3: the fraction of islands in a certain S-class on which a species occurs) may be influenced by competition. Thus, Connor and Simberloff's alleged 'null' model may contain all kinds of 'hidden structure' (see also Diamond 1982; Harvey et al. 1983; Quinn & Dunham 1983; Colwell & Winkler 1984; May 1984).¹⁰²

A third, related point of criticism is that the constraints used by Connor and Simberloff are so strong that there is little chance at all for the simulated distributions to deviate from the empirical ones. According to Diamond and Gilpin, Connor and Simberloff actually do little more than renaming islands and species, making their test empty (see also Grant & Abbott 1980). This holds especially for the checkerboard patterns. Though the probability of such a pattern occurring by chance is practically nihil, the method of Connor and Simberloff is unable to detect it as different from random distributions. Moreover, according to Diamond and Gilpin, Connor and Simberloff used too weak a statistical test, whence the chance of making a type II error (unjustly not rejecting the null hypothesis) is high (see also Toft & Shea 1983).

These points of criticism all relate to the method used by Connor and Simberloff, and hence to their criticism of Diamond's assembly rules A, E and G. Remarkably, Diamond and Gilpin hardly respond to Connor and Simberloff's criticism that rules B, C and D are tautologies, since Diamond provides no independent evidence of active resistance. In fact, the only thing they do is repeat Diamond's (1975a) 'evidence'. As to the criticism of rule F, that there are no islands with only two species and that therefore this rule is untestable, Diamond and Gilpin state that Diamond (1975a) had repeatedly made clear that his assembly rules pertained to guilds and not to entire avifaunas. Many islands in the Bismarck archipelago, as well as in the New Hebrides, contains two species of a guild.

13.4.4 An alternative null model

In spite of their criticism, Gilpin and Diamond (1982) take over Connor and Simberloff's method, be it that they don't use computer simulations but an analytic method to generate random matrices. They directly calculate the expected chance of a species occurring on an island, given that there are m species and n islands, that every species occurs on a fixed number of islands and that every island contains a fixed number of species. Thus, they retain Connor and Simberloff's constraints 1 and 2. Initially, they leave constraint 3 (the incidence functions) out. However, to show that this constraint may contain effects of competition, they

¹⁰²This is the reason why Connor and Simberloff's 'null' hypothesis is not a proper null hypothesis and has no logical primacy. A null hypothesis and an alternative hypothesis should be mutually exclusive and jointly exhaustive. Neither is the case with Connor and Simberloff's hypothesis and Diamond's (see also Sloep 1986, 1993).

later add it to their test. Next, they calculate for each possible species pair the expected number of shared islands. By assuming that these expected numbers are normally distributed, they can express the difference between the expected number and the empirical number of shared islands in terms of the standard deviation from the expected number. For 'random' communities this standard deviation is itself normally distributed, with mean 0 and standard deviation 1. Gilpin and Diamond use a X^2 -test to compare the empirical distribution of standard deviations with this normal distribution.

In all cases (Bismarck, New Hebrides and West Indies), there appears to be a significant difference between the empirical and the expected distribution. When adding constraint 3, the difference appears to be smaller - which Gilpin and Diamond take to indicate effects of competition - but is still significant. Strikingly, however, most deviations occur in a direction opposite to what one would expect had the species' distributions been affected by competition, namely in the direction of positive associations of species. According to Gilpin and Diamond, the explanation for these positive associations lies in the shared biotope preferences, geographical origins and distributional strategies of species, and in a number of single-island endemics.¹⁰³ They explain part of the (much smaller) number of negative associations in the opposite way, in terms of differences in geographical origin, dispersal strategies and biotope preference of species, and the remaining part in terms of, of course, competitive exclusion.

13.5 Rethorics

13.5.1 The guild that doesn't take stones into the gizzard

In an attempt at reconciliation, both parties to the controversy met at a conference organized by colleagues of Connor and Simberloff at the Florida State University, which was especially devoted to the role of competition and the testing of null hypotheses in ecology. The volume of contributions to this conference (Strong et al. 1984) contains a shortened version of the two papers by Diamond and Gilpin (Gilpin & Diamond 1984a), a reaction by Connor and Simberloff (1984a), followed by two 'rejoinders' (Gilpin & Diamond 1984b; Connor & Simberloff 1984b). Far from reconciliation, however, the parties apparently seem to drift ever more apart. Though the volume to the conference is entitled "Ecological communities: conceptual issues and evidence", the contributions by Diamond c.s. and Simberloff c.s. hardly deal with conceptual or empirical issues any more. The controversy becomes increasingly focused on who has the best null model. The dispute thereby becomes on the one side ever more technical and on the other side ever more fierce and rethorical, while conceptually or theoretically the standpoints remain essentially unchanged. For this reason, I will omit a discussion of the further course of the controversy. The only issue of interest is a discussion about the restriction to guilds.

Connor and Simberloff (1984a) complain that Gilpin and Diamond (1984a) have changed the original argument of Diamond (1975a). Of course one may reasonably expect competition to occur only between ecologically related species but Diamond's assembly rules said nothing about restriction to guilds. They further notice that confining the analysis to guilds is no easy

¹⁰³Endemics are species that have evolved on an island and, because of isolation, are found nowhere else. See also chapter 12.

matter, as it requires detailed data on resource use by all species in a community. They notice that "no one has yet been able to analyze all the guilds in a community, and at present we can deal only with a few guilds making up part of a whole community (Krebs, 1978)" (Connor & Simberloff 1984a, p. 319). According to Connor and Simberloff, for no guild, let alone for the entire avian community, have Gilpin and Diamond provided data to justify guild boundaries. The reply and counter-reply to this are typical of the tone which the dispute has by now received:

"The quote from Diamond (1975) omitted the word "guild" because Diamond (1975) had repeatedly made explicit (..) that his analysis was confined to guilds (..). Diamond considered it unnecessary to belabor this point in every possible quote about assembly rules, because it was not appreciated that anyone would be so silly as to search for effects of competition in all pairwise species combinations of a fauna (..). We did not waiste the entire length allotment of our paper to defining guilds and listing species because Diamond (1975) had already done so for each guild discussed, based on the technical literature on New Guinea birds. For example: "All [species of the fruit-pigeon guild] are ecologically similar in being arboreal, living in the crowns rather than in the middle story, being exclusively frugivorous, not taking stones into the gizzard, and hence restricted to eating soft fruits that can be crushed against the gizzard wall" (Diamond 1975, p. 406); species listed on pp. 407 and 408 (..); utilization functions presented on pp. 407 and 428-433; extensive dietary data published by Crome (1975) and others" (Gilpin & Diamond 1984b, p. 334-335).

Connor and Simberloff respond to this by stating that:

"Diamond (1975) cites no technical literature to justify the guild assignment on pp. 406-411, where the [fruit-pigeon] guild is defined, or anywhere else. Crome (1975) is not cited, nor is Crome acknowledged. Crome (1975) discusses only fruit-pigeons, so it is impossible based on Crome (1975) to say that the eighteen listed species constitute the guild of exclusively frugivorous arboreal species that do not take stones into the gizzard" (Connor & Simberloff 1984b, p. 342).

In addition, Connor and Simberloff keep hammering at the fact that even if one were able to delineate all guilds in a community, and even if one would find exclusive distributional patterns of species within guilds, he could still derive nothing from these patterns themselves about possible causes. They repeat that Gilpin and Diamond have provided no independent evidence for a role of competition, nor for their claim that their (Connor and Simberloff's) null hypothesis would contain 'hidden structure'. Gilpin and Diamond (1984b) repeat that this evidence is provided by Diamond (1975a).

13.5.2 Degenerate matrices and overweight people

Finally, there is an interesting exchange over Diamond and Gilpin's claim that Connor and Simberloff's method is unable to detect checkerboard patterns as non-random. Connor and Simberloff (1984a) state that the only example of a perfect checkerboard provided by Diamond and Gilpin (1984a), that of two species each exclusively occurring on four of eight

1	0	1	0	1	0	1	0
0	1	0	1	0	1	0	1

Figure 14: Example of a perfect checkerboard that cannot be changed if all columns sums are to be equal to 1.

then there is only one matrix (apart from shuffling rows and columns) possible. Of course, this is the one depicted by Diamond and Gilpin. It is no wonder, say Connor and Simberloff, that their procedure failed to recognize such a pattern as non-random, since they indeed ignore degenerate matrices. Furthermore, they reason, consider two 20 by 20 matrices, both perfect checkerboards, the first such each species occurs on ten islands, each island contains ten species and there are ten exclusive pairs, and the second with the same marginal totals as the first but with a hundred exclusive pairs. Clearly, the first matrix has a very low number of exclusive pairs relative to the possible number that might obtain, and its pattern is exactly opposite to what one might expect if competition were important. Therefore, "checkerboardness *per se* need not imply competitive exclusion, and it is not a virtue if an algorithm automatically finds any checkerboard to be improbable" (Connor & Simberloff 1984a, p. 323). If one wants to know what is the probability of ten exclusive species pairs in a random 20 by 20 matrix, given that all row and column sums are equal to ten, one would have to calculate how many different matrices there are with 0, 1, 2, etcetera exclusive pairs. Since Diamond and Gilpin have not done so, they cannot say how likely it is for the first checkerboard to occur by chance alone. Consequently, they have no grounds for saying that Connor and Simberloff's procedure is unable to recognize this matrix as non-random (though in fact, they note, their test does recognize this matrix as unusual).

The arguments are of no help, however. Gilpin and Diamond think they have found a perfect analogy to Connor and Simberloff's reasoning: "The man in figure 1 weighs 484 lbs., but we have found a man whom we show in figure 2 and who weighs 740 lbs. Clearly the man in figure 1 has a very low weight relative to the possible weight a man might have. So .. it is not a virtue if your algorithm automatically identifies the man in figure 1 as overweight" (Gilpin & Diamond 1984b, footnote on p. 336). In addition, they accuse Connor and Simberloff of attempting to hide the weakness of their test by introducing the term "degenerate matrices", with its mathematically and morally pejorative connotations. They state that there is nothing immoral to degenerate matrices, however, thereby giving Connor and Simberloff a shot at an empty goal. After the latter have lamented: "We are beginning to feel like Br'er Rabbit enmeshed in the Tar Baby: Each of our attempts to elucidate the statistics of species combinations on islands seems only to elicit a mass of obfuscatory goo" (Connor & Simberloff 1984b, p. 341), they end the discussion with the words

"Lest this exchange degenerate further (..), we state that "degenerate" has no pejorative connotations when assigned to matrices (..) and is used in matrix algebra (..) without connoting moral or mathematical turpitude. We felt it was apparent that non-existent

possible islands (see figure 14), points to non-random colonization only when viewed alone without fixed column sums (constraint 2). The probability of this pattern occurring by chance alone is indeed, as asserted by Diamond and Gilpin, almost nihil. However, when degenerate matrices (that is, matrices in which species or islands have 'disappeared' because their row or column sums, respectively, are zero) are not allowed, its probability becomes 1, because

species (..) and empty islands (..) could tell us nothing about forces constraining species co-existence, so that matrix rows or columns representing such species or islands should be omitted. (..) In any event, no statistical statement can be made about matrices or overweight people without some notion of the nature of the universe. An extra-terrestrial who saw but two humans would have no way of knowing whether a 484 lbs. man is heavy or light " (Connor & Simberloff 1984b, p. 342-343).

13.6 The great misunderstanding

13.6.1 Results of the controversy

The fierce and increasingly rethorical tone of the dispute may lead one to suspect that the controversy has lasted on all points. They obscure, however, that on major issues a reasonable degree of agreement has been reached.

This concerns first of all to the method of testing null hypotheses. Although disagreement remains as to the exact way in which null models are to be formulated, the method in itself is accepted and applied by Diamond c.s. On the other side, Simberloff c.s. admit that their null hypothesis is not a proper null hypothesis in the statistical sense and, hence, has no logical primacy over other hypotheses. Other ecologists who have become involved in the controversy also agree that the testing of null hypotheses is in principle a useful method, but that formulating a proper null model is no easy matter (see Wright & Biehl 1982; Harvey et al. 1983; Quinn & Dunham 1983; May 1984).

After, and probably because, agreement has been reached on the level of method, the parties also come to agree on the level of (cognitive) content. On the one side, Simberloff c.s. are forced to admit that the species composition of communities as a whole deviates considerably from random. They admit in particular that in the cases of the West Indies birds and bats their null hypothesis must be rejected (Connor & Simberloff 1984a). On the other side, Diamond c.s. admit that only a small fraction of the deviations may or need be attributed to competition. In fact, the only points of dispute remaining in 1984 are the evidence for competition in these cases, and some technical details concerning null models. As far as I know, the final contribution to the controversy is a paper by Connor and Simberloff from 1986. This paper is a summary review of the controversy (and others; see below) and, apart from a further discussion of the statistics of null hypotheses, adds nothing to their points of view in 1984.

13.6.2 The domain of competition theory

When we look at the origin of the controversy in the light of its outcomes, the first thing appearing is an enormous misunderstanding of what competition theory is supposed to explain. As I have shown, Diamond (1975a) could explain the larger part of the incidence functions in terms of properties of individual species and islands. In only 13 of the 141 cases - the supertramps - did he appeal to competition theory. On the other hand, he larded his entire paper with claims about the unique interest of competition in structuring whole communities. And though on the one hand he clearly indicates that his assembly rules pertain only to guilds, on the other hand he strongly suggests that they are important for communities as a whole. This is also evident from the title of his paper: "Assembly of Species Communities". The extravagance of these claims is out of all proportion to the moderate

content of the rest of his paper. It is also out of proportion to the domain of the competition theory he so fervently defends. This theory pertains only to ecologically related species exploiting the same resources. Mostly, by far not all species in a community are competitors, especially not in bird communities, and it is absurd to suggest that competition could be responsible for the whole structure of communities.¹⁰⁴

It is the extravagant claims of Diamond that give rise to the misunderstanding of Simberloff c.s. that the assembly rules apply to all species in a community, and that competition is supposed to explain the whole structure of communities. The larger part of the controversy is devoted to the removal of this misunderstanding. The turning point comes when Diamond and Gilpin (1982) reproach Connor and Simberloff (1979) of having performed their analysis on whole species sets, whereas it should have been restricted to guilds. The agreement on this point is further reinforced when Gilpin and Diamond's test also shows that merely a few of the deviations from the random distribution are negative associations of species. That problems remain in the field of delineating guilds and evidence for competition does not detract from this agreement.

13.6.3 Holism and reductionism

This explanation leads to the question, however, what moved Diamond (1975a) to make such extravagant claims. The answer to this question is enclosed in the nature of these claims. As we have seen (13.2.2), Diamond is of the opinion that communities are stable, integrated entities whose structure cannot be explained fully in terms of the properties of their component species: "do the properties of each species considered individually tell us most of what we need to know in order to predict how communities are assembled from the species pool? (..) the answer is "No"." (Diamond 1975a, p. 385-386). In other words, the whole is more than the sum of its parts. Diamond's holistic view of communities appears also from his approval of a claim by Levins (1975) that "the course of natural selection in a particular species may not be comprehensible without reference to the whole matrix of community interactions" (Diamond 1975a, p. 385).

It is this holistic as well as his deterministic view of communities that brings Diamond to the formulation of assembly rules. He interprets the fact that certain combinations of species occur less often than expected as if these combinations are 'forbidden', and 'forbidden' means 'excluded by competition'. He calls existing combinations 'permitted', and 'permitted' combinations are 'stable', that is, 'resistant against invasions by competitors'. His other explanations of the incidence functions are also largely based on deterministic factors (island area, biotope diversity, food supplies), and he sees only a small role for chance processes in colonization on a first-come-first-served basis and in the increased extinction chances of small populations.

¹⁰⁴To this may be added that competitive exclusion is only one of the possible outcomes of competition, and one that is expected to occur only in extreme conditions. Most often, the effects of competition are far less severe, and competitors may well be able to coexist. See chapter 11.

Simberloff, on the other hand, is an outspoken reductionist and probabilist. His suggestively entitled paper, "A succession of paradigms in ecology"¹⁰⁵ (Simberloff 1980), is one long tirade against what he (not always adequately; see Grene 1980) calls holism, idealism¹⁰⁶ and essentialism in ecology, and a defense of reductionism, materialism and probabilism. In his view, communities are nothing but random assemblages of species, the product of stochastic colonization and population dynamic characteristics of species (Simberloff 1978, 1980).

To this should be added that the controversy between Diamond c.s. and Simberloff c.s. is not an isolated dispute, in which case it could be seen as relatively insignificant, but forms part of a much broader controversy about the role of competition in ecology.¹⁰⁷ Simberloff and his colleagues are involved in a true crusade against what in their view are unjust or premature applications of competition theory. Beside the controversy over Diamond's assembly rules, there are specific controversies about the number of species on islands¹⁰⁸, the species composition of island communities¹⁰⁹, the species/genus ratio on islands¹¹⁰, and the phenomenon of character displacement on islands¹¹¹. In all these cases, the strategy of Simberloff c.s. is the same: one should always first test the null hypothesis that the phenomena to be explained are not the result of chance processes, given the population dynamic characteristics of species, and only when and after this hypothesis has been rejected look for alternative, biological explanations. In 1986, Connor and Simberloff explain once more what they mean: "a null hypothesis is one that posits no effects, a conjecture that nothing in the data at hand (...) would lead one to propose an explanation other than chance

¹⁰⁵Succession is the term ecologists use for particular forms of development of communities and ecosystems, involving the replacement of one set of species by another. The "succession of paradigms in ecology" as depicted by Simberloff is the analogous replacement of holistic succession theories, such as Clements's (1916, 1936), by reductionistic ones, such as Gleason's (1939, 1962).

¹⁰⁶He means by this ideal-typical or typological thinking: community types as natural kinds.

¹⁰⁷See Grant & Abbott 1980; Strong 1980; Alatalo 1982; Schoener 1982; Wright & Biehl 1982; *The American Naturalist* (122) 1983; Case & Sidell 1983; Harvey et al. 1983; Grant & Schluter 1984; May 1984; Strong et al. 1984; Diamond & Case 1986; Sloep 1986, 1993. See also Lewin (1984) and note 88.

¹⁰⁸Among others, Simberloff 1970; Connor & Simberloff 1978; Connor & McCoy 1979; Gilbert 1980; Sugihara 1981; May 1984.

¹⁰⁹Among others, Grant & Abbott 1980; Ricklefs et al. 1981; Simberloff & Boecklen 1981; Strong & Simberloff 1981; Bowers & Brown 1982; Collwell & Winkler 1984.

¹¹⁰Among others, Grant 1966; Simberloff 1970, 1983; Connor & Simberloff 1978; Grant & Abbott 1980; Järvinen 1982.

¹¹¹Among others, Lack 1947; Brown & Wilson 1956; Grant 1972, 1975; Strong et al. 1979; Strong & Simberloff 1981.

for the observed result. In the sense used here, *chance* is not meant to imply the absence of deterministic forces acting to produce the observed result; (..) It does mean that, whatever the forces are that determine each species' distribution, there are no reasons from the geographical data themselves to conclude that among those forces is the presence or absence of other species" (Connor & Simberloff 1986, p. 159-160).

13.7 Other factors in the controversy

13.7.1 Ecology and nature conservation

One of the reasons for the sensitivity and persistence of the holism-reductionism issue in ecology is that, beside cognitive aspects, it also has ethical, esthetical and psychological aspects. These relate to differences in conceptions of nature and associated motives and strategies for nature conservation (van der Windt et al. 1987).

In exoteric (*sensu* Fleck 1979) circles of organismal biology, the holistic claim that the whole cannot be reduced to its component parts is often linked to the view that it is ethically inadmissible to cut up or otherwise manipulate living organisms. Analogously, holism in (both esoteric and exoteric circles of) ecology, the idea of harmony and wholeness of nature, is often linked to the idea of the balance of nature, that must not be disturbed and hence should be protected (Egerton 1973; Worster 1977; McIntosh 1980, 1985; Achterberg & Zweers 1984; van Koppen et al. 1984; Achterberg 1989). A holistic and deterministic view of nature seems to offer more and better perspectives for nature conservation than a reductionistic and probabilistic view: if natural systems behaved according to fixed and predictable patterns, there would be more opportunities for control and regulation than there would be if they were unpredictable and idiosyncratic (see also Kwa 1984, 1989). Simberloff himself points to a psychological factor why his view may be unattractive to some: "Certainly there is something profoundly disturbing about a nature in which random elements play a large role. (..) the idea of an unbalanced, stochastically driven natural community inspires distrust" (Simberloff 1980, p. 90).

A good example of the relation between holistic ecology and nature conservation is the International Biological Program (IBP). This was a large-scale and influential research programme in the 1960's and 1970's on ecosystems all over the world. The IBP was fully based on Odum's (1969) holistic systems ecology and was aimed at nature conservation, environmental control and management of natural resources. On the other hand, it has had an enormous influence on the growth of (systems) ecological knowledge (McIntosh 1974, 1980, 1985; Simberloff 1980; Kwa 1984, 1989). According to Simberloff (1980), the IBP was the heaviest subsidized ecological research programme so far. He notes that for this (economical) reason alone, the holistic systems approach was very tempting, apart from philosophical or biological considerations (Simberloff 1980, pp. 28-29).

It is likely that interests in nature conservation are also effective in determining Diamond's position in the present controversy. At the time at least, Diamond worked also as an advisor to the governments of various countries in the Pacific on the design of nature reserves and the preservation of indigenous flora and fauna (Diamond 1978, p. 322). A direct clue for this interest is found in another controversy between Diamond c.s. and Simberloff c.s. which concerned applications of MacArthur and Wilson's (1967) equilibrium theory to the design of nature reserves. As we have seen in the former chapter, this theory can be used to explain the species-area relation: the larger an area (island), the higher the number of species it

contains. Diamond (1975b, 1976) and Terborgh (1975, 1976) appealed to the theory in a plea to create as large as possible nature reserves. They were criticized by Simberloff and Abele (1976a,b) who found that the theory had as yet been insufficiently tested, let alone proved, and who also argued that the theory may just as well be used to justify the creation of many smaller reserves instead of one large reserve.¹¹²

The resemblance with the other controversy is striking. Diamond is quick to use an attractive though yet immature theory, and it is also clear from what interests he does so, while Simberloff warns against such premature applications.

Of course, all this is not to say that autecologists or population ecologists such as Simberloff could not be nature conservationists, only that, at least for the time being, their ecology lends itself less well for conservation purposes. Opportunities for applications of autecology or population ecology in the field of nature conservation and management seem to lie more at the level of the protection of individual species, but this form of nature protection is just recently gaining attention (Looijen et al. 1989; Wiersinga et al. 1989).

13.7.2 Professional interests

The question remains why the controversy lasted so much longer in spite of the agreement that was reached on the methodological and conceptual level. Two factors are probably responsible for this, namely the complexity of null models and the influence of professional interests.

As a matter of fact, since 1982 the controversy no longer concerns the role of competition or Diamond's assembly rules, but becomes focused at technical details of null models. I have already mentioned that by then the parties to the controversy had come to agree upon the general use of testing null hypotheses, but not upon the precise form that null models should have. This appears to be an extremely difficult issue. On the one hand, one needs to incorporate constraints such as the ones used by Connor and Simberloff to lend some biological realism to the null model. On the other hand, this always presents the danger of introducing into the null hypothesis all sorts of hidden effects, among others of the factor against which the null hypothesis is to be tested. The question is, however, whether at this point we should still talk of a controversy or rather of a discussion of how to solve a difficult methodological problem, a problem, moreover, that both parties have to deal with.

A second factor that may be responsible for the at least apparent persistence of the controversy is formed by the professional interests which the opponents have in the succeeding of their respective programmes. Diamond's notion of competitively induced assembly rules has received a serious blow from the criticisms by Simberloff c.s., and with their 'improved' null model Diamond and Gilpin attempt to save as much as they can of what is left of the possible role of competition. Incidentally, a paper by Gilpin and some other colleagues (Gilpin et al. 1986; and see also Roughgarden 1989) shows that the idea of assembly rules has not been completely abandoned. In this paper competition theory is used, analogous to Diamond (1975a), to explain assembly rules for communities of *Drosophila* species. An crucial difference with Diamond (1975a) is, however, that in this case the

¹¹²A nice detail in this context is, of course, that Simberloff was one of the few researchers who found empirical support for the equilibrium theory (see chapter 12).

communities consist of both taxonomically and ecologically closely related species among which interspecific competition may indeed be expected.

That the position of Simberloff c.s. is also being steered by professional interests becomes likely when we consider that they have put all their stakes on the null programme. In both controversies with Diamond c.s., Simberloff seems to take the position of the puritan scientist who guards against rash conclusions and watches over scientific method.¹¹³ Though at first sight this may be seen (as it is most certainly seen by Simberloff himself) as a defense of intrinsic scientific interests, in the course of the controversy it becomes more and more a matter of personal interests. Simberloff c.s. have invested heavily in their programme and it is quite understandable that they head for defense when their null model is being attacked.

The influence of professional interests is probably even reinforced by the fact that, considering institutional ties, they take the form of group interests. The anti-competitionists (Simberloff, Connor, McCoy, Strong, Abele, Boecklen, and Thistle) are (or were at the time) all connected to the Florida State University. The competitionists are, with some exceptions (Roughgarden, Dunham, Harvey and Silverton), connected to the University of California (Diamond, Gilpin, Schoener, Quinn, Colwell, and Winkler) and to Princeton University (Terborgh, Grant, Schluter, Abbott, and May).

It will be clear that these different interests are not causes of the controversy. They do seem to perpetuate the arguments, however. A strong clue for this is the fact that the dispute becomes ever more fierce and rhetorical, while on the level of content some rapprochement occurs. The function of this seems to be to hide the fact that concessions to the other side have been made, that one has retreated from earlier standpoints, and to keep as much right as possible in one's own camp.

13.7.3 Competition as ideology

A last factor that seems of interest to the controversy is the influence of ideology. Diamond (1978) makes an interesting attempt to point out that interspecific competition is even more important in nature than one would expect from distributional patterns of species. Suppose, he argues, that as an economist one would make the same mistake, namely to observe different species, all having similar niches but rarely ever actually fighting, and to conclude that interspecific competition is unimportant. He would go, for example, to the Acuma desert and notice that all extant nitrate mines are located in Chili instead of Peru or Bolivia, and that peace reigns. If he had read no history book, he wouldn't realize that some hundred years ago these three countries were involved in a short but heavy battle, that Chili won the war and thereby settled competition over nitrate for the next century. Or he would see Herz and Avis next to each other at the airport. He would observe that the ladies in yellow don't fight at all

¹¹³The flesh is weak, however. Although they are later forced to admit that their null hypothesis must be rejected for the West Indies birds and bats (Connor & Simberloff 1984a), they initially conclude to the opposite, even though the empirical distribution of the species deviates significantly from the simulated random distribution (see 13.3.2). That they thereby violate the very falsificationism they so fervently advocate may be seen as a typical specimen of 'confirmation bias' (Loehle 1987). This too may be a matter of defense of professional interests.

with the ladies in red, and he would conclude that Herz and Avis do not compete. In reality, however, they compete strongly, of course, but the mechanism is exploitation of resources - customers - and not fighting. Or, finally, he would notice that RCA today makes no computers, whereas IBM does, and he would conclude that competition is unimportant in computer business. If he hadn't watched the business, he wouldn't realize that RCA once did make computers but that IBM was so much more successful in attracting customers, without taking recourse to fight, that the competition battle was settled with the permanent exclusion of RCA from the computer market (Diamond 1978, p. 329). It is evident that ideological background serves here to justify ecological theorizing (without any relevance, however, to the truth value of competition theory).

Another example is provided by Simberloff (1980). According to Simberloff, the paradigmatic status of the holistic ecosystem concept is due to the fact that "it provides support for the notion of self-regulatory powers inherent in unfettered capitalism (...). For if a community of organisms, naturally selected each to maximize the representation of its own genes, can be shown to be analogous to a single organism whose parts all work to a common purpose, so ought competitive capitalism to produce a unified whole which benefits all. This is an old notion: Adam Smith's metaphor was that of a hidden hand converting the profit-maximizing activities of individuals into the good of the whole" (Simberloff 1980, p. 28). He adds to this, however, that "Perhaps the most convincing argument that the main attraction of holism is not as a subtle justification of capitalism is that it has adherents with long-standing, impeccable Marxist credentials (e.g. Levins 1968, Lewontin and Levins 1976)" (Simberloff 1980, p. 28). No wonder that the reply comes from Levins and Lewontin (1980).

13.8 Conclusions

I have shown that the controversy between Diamond c.s. and Simberloff c.s. is underlaid by profound differences of opinion that go back to the contradistinction between a holistic-deterministic view of nature and a reductionistic-probabilistic one. These different conceptions of nature lead not only to cognitive but also to methodological differences. Diamond worked inductive-confirmatory. He sought for patterns in the assembly of communities that agreed with competition theory, found these patterns in mutually exclusive species pairs and other combinations and thereby saw his theory confirmed. Simberloff c.s., on the other hand, use (or claim to use) the hypothetico-deductive method. They start with individual species and islands and are prepared to accept a role of competition only when the null hypothesis must be rejected, and they demand independent testing of competition theory.

I have further shown that the controversy is steered also by various professional, social and ideological interests and backgrounds. A holistic-deterministic approach in ecology is tempting against the background of a technical knowledge interest in nature conservation and management. The importance of competition in ecology is justified by an appeal to the role of competition in economics. In addition, the controversy is being influenced by differing views on scientific progress. The anti-competitionists defend their strategy by appealing to falsificationism, an appeal which is more or less rejected by the competitionists. Finally, the course and nature of the controversy become ever more influenced by professional interests.

Because in time the dispute becomes increasingly more fierce and rethorical, it looks as if the controversy lasts on all fronts, but that actually holds only for the delineation of guilds and the proof of competitive exclusion. On the cognitive level, however, agreement is reached

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on the following points: (a) the patterns in the species composition of communities are not completely random, that is, are not the mere result of stochastic processes; (b) the patterns can be explained largely in terms of properties of individual species and island characteristics; and (c) in only a small number of cases an appeal to competition theory can or must be made.

When we view these results in terms of the origins or causes of the controversy, two things are striking. First of all, not a single brick is left standing of the holism-reductionism edifice. The fact that the structure of the communities is significantly non-random (point a) means that there are holistic (emergent) patterns that require investigation and explanation. Further, the explanations offered are largely reductionistic or reductive (point b) and there is only a small residue that may require 'holistic' explanation (point c). In addition, the explanatory factors are partly deterministic, such as island area, biotope diversity and food supplies, and partly stochastic, such as immigration and extinction chances, which in turn depend on the dispersal abilities and population dynamic characteristics of the species and on the size and degree of isolation of the islands.

The second most striking thing about the controversy is that the results mentioned under points (a), (b) and (c) above are in very close agreement to Diamond's (1975a) initial moderate account (see 13.2.2). In other words, one has required ten years of discussion mostly to reconfirm what (the moderate) Diamond stated already in 1975. Why then the entire discussion? The reason lies in the extra claims of Diamond (1975a), the heavy stress he put on holistic integration of communities, the weight he gave to his assembly rules, and the exclusive role he assigned to competition. It is such heavy and extravagant claims that perpetually blow new life in the holism-reductionism dispute in ecology, without there being good reasons for it. They are eliminated, therefore, in the course of the controversy.

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The main thesis of this book was that holism and reductionism should be seen as mutually dependent and co-operating research programmes instead of incompatible views of nature or of the relations between sciences. Holism and reductionism are incompatible only in so far as there are holists who claim that wholes cannot be analysed at all, and reductionists who claim that there are no wholes other than, say, atoms to study at all. These claims are so absurd, however, that they are not worthy of discussion.

As for the remaining elements of both doctrines, I have argued that none of the major tenets of holism - the emergence thesis, the need to study wholes phenomenologically, and the need for functional explanations in biology - actually conflicts with the major claim of reductionism, that higher level laws and theories can be reduced to lower level ones. The emergence thesis is a valid ontological thesis, but it does not contradict the (epistemological) reduction thesis. Functional explanations are indispensable in biology, but they are essentially causal and therefore neither violate the principle of causal determinism nor stand in the way of reductions. Finally, because of emergence and because there must be something to reduce before we can have reductions, the holistic or phenomenological study of wholes is a prerequisite for the possibility of reductions.

I have used two philosophical models to further support my thesis, viz. Kuipers's reduction model and Zandvoort's model of co-operating research programmes. According to Kuipers's model, heterogeneous micro-reduction is the explanation of a macro-law or -theory by a micro-theory supplemented with (at least) an aggregation hypothesis and a transformation (correlation or identification) hypothesis. The structure of such reductions alone already indicates that, in terms of research programmes directed at the whole and its parts, respectively, holism and reductionism do not exclude each other but rather complement each other. For they require that there be both macro-laws or -theories to be reduced and reducing micro-theories, as well as connecting bridge principles. That is, they require the fruits of both holistic and reductionistic research programmes. According to Zandvoort's model, moreover, research programmes that are directed at different levels of organization are often mutually dependent and (asymmetrically) co-operating programmes. Though each may be independent of the other as far as its own level is concerned, they are mutually dependent when it comes to relations between levels. As it is unlikely, moreover, that macro-laws or -theories can be constructed on the basis of micro-theories alone, the relationship is most likely to be one of asymmetric co-operation: in providing macro-laws or -theories that call for deeper explanations, holistic programmes act as guide programmes for reductionistic programmes, while reductionistic programmes, if they succeed in providing the explanations, act as supply programmes for holistic programmes. I have discussed several examples of heterogeneous micro-reduction, also in biology and ecology, illustrating my thesis.

There are some interesting problems and questions remaining to be investigated, however. These problems and questions pertain to (1) the specificity of ecological laws, (2) reduction to more than one micro-theory, and (3) the possible relationship between (1) and (2).

In the first place, the present reduction model requires that there be general laws and theories, both on the macro-level and on the micro-level. As noted in chapter 8, however, general laws and theories are hard to come by in ecology, especially at the macro-level of communities (and ecosystems). I have pointed to the ambiguity of the term 'community' as a possible cause, reasoning that if different researchers study different kinds of objects but all report to be studying communities, the chances of general patterns (laws) being abstracted from these studies are smaller than if they would all be studying the same kind of objects.

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On the other hand, of course, even a precise and unambiguous definition is no guarantee to the discovery of general laws and theories about communities. A critic might argue, moreover, that the causal relation could also be the other way around: because there are no general laws and theories about communities, ecologists (are free to) use the term 'community' for various different kinds of objects.

The question is, however, what one could possibly mean when stating that there are no general laws and theories at the level of communities. He could mean two things: (1) 'out there', in nature (that is, ontically), there are no general laws at the level of communities; or (2) ontically, there are general laws at the level of communities but we don't know them yet. In case (2), the present lack of general laws and theories about communities is due to epistemic factors, and all we can do is to await the results from more research. In this case, the (re)definition of the term 'community' proposed in chapter 9 (the set of individuals of two or more species occurring in the intersection of the areas occupied by populations of these species), may help. In case (1), there are two sub-possibilities: (1a) ontically, there are no general laws at the level of communities, because there are no such things as communities; or (1b) there are such things as communities but they are not subject to general laws. Whether or not case (1a) obtains is, of course, the major issue of the holism-reductionism dispute in ecology. There can be no doubt that there 'really' (ontically) are communities in the sense of the definition proposed in chapter 9. As noted, however, this definition is neutral with respect to the question whether communities are 'mere' aggregates of organisms or supra-individual wholes. Shortly before this book went to press, an anonymous reviewer pointed out to me that if communities are supra-individual wholes, if only weakly cohesive ones, they must have a non-trivial emergent structure determined by interactions between the individuals. As an example, he mentioned that within one city there are many different social systems, which are determined by the interactions between the individuals. I agree that there must be some relations between the parts (individuals), some bondings, however weak, in order for communities to be more than mere aggregates. In chapter 9 I argued, however, that interaction is neither a necessary nor a sufficient condition for community membership. The question is, however, what we mean by interactions, relations or bondings. In terms of the kinds of interactions recognized in ecology, humans need not compete or prey upon each other in order to belong to a social system ('community'). Nor do they necessarily have to be commensalists or even mutualists. All that is required is that they share the same space and have a good time together (share the same work, hobbies, friends, interests). A most interesting question is whether this is not also sufficient in the case of ecological communities. That is, is it not sufficient that organisms have similar ecological preferences, requirements and tolerances in order for the communities to which they belong to be more than mere (trivial or random) aggregates? Don't such shared preferences, requirements and tolerances constitute sufficient *bonding relations* between individuals? On the other hand, are they sufficient to make communities into supra-individual wholes (if not by definition)? If not, are social systems supra-individual wholes, then, and why? Do interspecific interactions, such as competition and predation, make for stronger or for weaker bondings? What if one individual eats the other, or if one individual competitively excludes the other?

These are very interesting questions for follow-up research. However, I think that, whatever the answers to these questions, the community concept should be defined independently of those answers. For both shared preferences, requirements and tolerances of individuals and interspecific interactions may constitute a major part of *explanations* of community structure.

Therefore, they should not be included in a *definition* of the concept of a community. For the same reason, I think that community *structure* should be defined, at least for the time being, simply (as is done presently) in terms of species composition, and that it should be left to theories about relations between species and environments, and about interactions between species, to explain this structure.

Case (1b), finally, seems to me to be highly unlikely, because if there are communities (in either of the above senses, or at least in the sense of my definition), then there are likely to be community types and, hence, general laws applying to or governing those types. (Inadequate though they may be in some respects, present classification systems indicate that there do exist such types.) The point may be, however, that those laws will not be 'universal' laws, but specific ones. In chapter 7 I have noted that biological laws are often restricted or specific in that they have a relatively small domain or reference class. For example, the Bohr-effect applies only to hemoglobin-carrying animals, and the laws of photosynthesis apply only to autotrophic plants. What applies to biological laws in general would seem to apply *a fortiori* to ecological laws in particular. As the level of organization increases, systems become more complex as more factors come into play. It may well be that, as a result, their behaviour becomes ever more idiosyncratic and the laws governing their behaviour become more specific. For example, there are different, specific laws (models of modern niche theory) for consumers of self-reproducing resources than there are for consumers of non-self-reproducing resources. The values of c and z in the relation ('law') between species number and area, $S = c.A^z$, are different for different taxonomic groups (though both examples indicate that there may still be more general laws underlying the specific ones). Thus, it may well be that laws at the community level are more specific than laws at the species level. And it may well be that there are different laws for, say, plant communities than there are for bird or insect communities. Once again, however, whether and to what extent this is the case is an empirical issue which can be settled only by more empirical research. And in this case, too, my definition of the community concept may be helpful in finding out how regular patterns in species' co-occurrences are.

In the second place, according to the present reduction model, reductions always involve one single reducing theory (supplemented by auxiliary hypotheses). The reduction of the Bohr-effect discussed in chapter 6 complies with this model, even though it involves two micro-theories. For, as I have shown, it actually consists of two heterogeneous micro-reductions, and each of them is still a reduction to one micro-theory. It seems more likely, however, that in ecology reductions will generally be established on the grounds of several, more or less complementary, and more or less equally important, micro-theories. The reduction of the Lotka/Volterra competition model to modern niche theory is a proper example of heterogeneous micro-reduction in ecology, complying with Kuipers's model. However, it is not a reduction of a theory at the community level, whereas this is (along with the level of ecosystems) the macro-level of major interest in ecology. Also, it seems unlikely that modern niche theory alone will be sufficient to explain the entire structure and dynamics of communities. Modern niche theory applies only to resource utilization, and specific models of the theory apply only to interactions between predators and prey or to interactions between competitors. However, the structure and dynamics of communities may be determined by many factors other than, or in addition to, interspecific interactions. The least that seems additionally required is a theory about the environmental requirements and tolerances of species (that is, habitat theory as discussed in chapter 10) on the one hand and environmental

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heterogeneity and biotope diversity on the other.

The results discussed in chapters 12 and 13 point in the same direction. Concretizations (approximative reductions) of MacArthur and Wilson's equilibrium theory involve several factors (and, hence, theories specifying those factors) in addition to island area and distance, such as species' dispersal abilities in relation to island distance; species' environmental requirements and tolerances in relation to biotope diversity of islands; endemism; and, possibly, interactions between species. As noted in chapter 13, Diamond used several, complementary theories to explain the structure (species' number and composition) of his communities, such as MacArthur and Wilson's equilibrium theory (area- and distance-effect), theories about biotope diversity, geographical origin of species, endemism, dispersal strategies and abilities, foraging strategies, niche theory and competition theory.

Thus, it seems likely that micro-reductions in ecology generally involve more than one single reducing theory. Although this doesn't affect the model of co-operating research programmes, nor my thesis about the co-operation of holistic and reductionistic programmes (both allowing several different programmes to co-operate), it has far-reaching consequences, of course, for the present reduction model. For it would mean that reductions can be much more (or even more) complicated than is presently assumed. It will be difficult to assess the precise role of each of the reducing theories, and it will also be much more difficult to assess the different roles played by reducing theories and auxiliary hypotheses (bridge principles). But the major consequence would be, of course, the implications for the idea of unification through theory reduction. The only way in which the idea could be rescued would be to show that the reducing micro-theories in ecology could themselves be reduced to one single (deeper) micro-theory, an unlikely prospect (though perhaps the task could be accomplished by the theory of natural selection).

Finally, there could be an interesting relation between the two main points mentioned above, that is, (1) specificity of ecological laws and (2) reduction to more than one micro-theory. For if ecological laws are specific, and if laws at the macro-level are more specific than laws at the micro-level, it seems likely that one will have to use several laws or theories at the micro-level to explain a law at the macro-level. If there are specific laws governing the behaviour of species (individuals of species), then it is likely that the behaviour of multi-species communities is the result of an interplay of several of such laws. Hence, one may have to use several laws or theories at the micro-level to explain a law or theory at the macro-level (communities).

The two problems, and the possible relation between them, form interesting subjects for future research.