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### Holism and reductionism in biology and ecology

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## CHAPTER 12 IDEALIZATION AND CONCRETIZATION IN ISLAND BIOGEOGRAPHY<sup>90</sup>

### 12.1 Introduction

In this chapter I will discuss another example of co-operation of holistic and reductionistic research programmes in ecology. The example concerns some developments in island biogeography, a branch of ecology dealing with the distribution and abundance of species on islands. This branch went through a phase of rapid development when MacArthur and Wilson (1963, 1967) introduced their equilibrium theory of island biogeography. Before that, island biogeography consisted mainly of a large collection of 'facts' (data, records) in which only a few regularities were observed. MacArthur and Wilson presented a simple holistic model about the number of species on islands which not only explained these regularities but also made a number of new predictions. In doing so, the model not only brought unity to the field but also generated an enormous amount of research. After a phase in which the model was tested, it appeared to be a bit too simple, however, and research became more focused at seeking out the various causal factors that might underlie the (parameters of the) model.

As argued by Haila and Järvinen (1980), these developments can be described very well in terms of the model of idealization and concretization (Krajewski 1977; see also Nowak 1980). Since concretization is more or less the same as approximative reduction (see chapter 3), they can be described also in terms of approximative reduction. MacArthur and Wilson's model appears then as a holistic idealization which subsequent reductionistic research programmes have concretized, that is, approximately reduced. Thus, in this structure of idealization and concretization we can recognize yet another form of co-operation of holistic and reductionistic research programmes.

### 12.2 The theory of island biogeography

#### 12.2.1 Area effect and distance effect

Islands and island biota have long fascinated biologists. It is known of Darwin that he derived many of the ingredients for his theory from island biota. One of the reasons for this special attention for islands is that they come a long way towards reaching the ideal of discrete, well-defined entities. As discussed in chapter 9, the major problem on the mainland has always been that the boundaries between communities are generally vague. On islands, it is a lot easier to determine the structure (number and composition of species) of communities (though as island size increases the same problem occurs).

One of the most striking features of island communities, and one of the first 'facts' of island biogeography (Hooker 1866), is their 'impoverishment' relative to communities in similar areas on the mainland. This impoverishment is found in both the total species number, the number of species per genus, and the number of genera per family. Because it is more pronounced on more distant islands, this phenomenon has been called the *distance effect*. In most cases, this effect can be readily explained through differences in dispersal abilities of species. For example, the absence of large predators on many islands can be explained from the fact that they are simply incapable, either physically or psychologically, to cross vast

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<sup>90</sup>This chapter is largely based on Looijen (1984). Since then, little has happened in island biogeography to affect my thesis.

stretches of water. On the other hand, many plant species have very light seeds or spores which can easily be carried by winds over large distances. Birds generally have good dispersal abilities, but even within this taxon there are large differences between species, genera and families. An extreme example is the difference between albatrosses, which can travel enormous distances, and penguins which have completely lost the ability to travel by flight.

Another long-known fact of island biogeography is the so-called *area effect*: the larger an island, the higher its number of species. Unsurprising as this may seem to a layman, there has always been considerable disagreement amongst ecologists (biogeographers) as to the precise nature of this relation (Arrhenius 1921; Gleason 1922; Fisher, Corbet & Williams 1943; Williams 1946; Preston 1948, see also May 1975; and Williamson 1981; see also section 12.2.3) as well as its explanation. In 'classical' island biogeography the area effect was mostly explained as an effect of biotope ('habitat') diversity<sup>91</sup>: smaller islands are generally less varied in environmental conditions, such as relief, elevation, fresh water, or vegetation cover, than larger islands. Since each species has its own specific environmental requirements and tolerances, different species may require different biotopes for their survival and reproduction. When certain biotopes are absent on small islands, then so are the species of these biotopes.

However, this is not the only possible explanation of the area effect. An alternative explanation was provided by MacArthur and Wilson (1963, 1967). MacArthur and Wilson introduced a simple<sup>92</sup> model, called the *equilibrium theory* of island biogeography, with which they could explain not only the area effect but also the distance effect, and also make a number of new predictions.

### 12.2.2 MacArthur and Wilson's equilibrium model

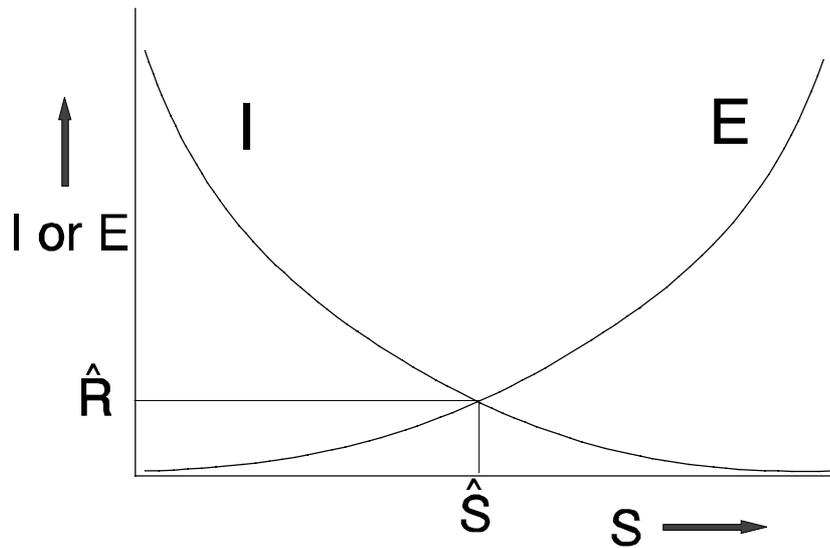
MacArthur and Wilson state that the number of species on an island is determined by two processes: immigration and extinction. They assume that as the number of species increases, the immigration rate decreases and the extinction rate increases. They also assume, and this is the crucial assumption of their theory, that on every island an equilibrium will be reached in the number of species as a result of a balance between the immigration rate and the extinction rate. The equilibrium is a dynamical equilibrium, however, since the number of species stabilizes but the species composition may (will) change continually. Finally, they assume that the immigrate rate is determined only by the island's distance to the mainland (or another potential source of immigrants) and that the extinction rate is determined only by the island's area. The more isolated (distant) an island, the lower the immigration rate, and the larger an island, the lower the extinction rate. The reasoning behind the former relation is that the more isolated an island, the smaller the number of species that are able to reach it (because of differences in dispersal abilities of species) and also the longer it takes for species that are able to reach the island to actually do so. The reasoning behind the latter relation is that the larger an island, the larger the population sizes of the present species and the smaller their chances of becoming extinct due to stochastic fluctuations in the number of

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<sup>91</sup>The classical term for this is habitat diversity, but see chapter 10.

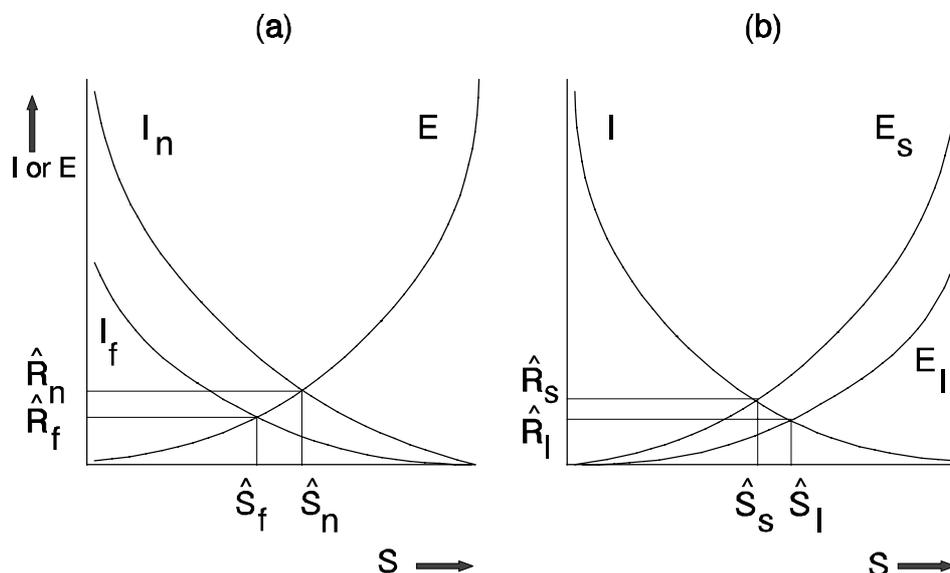
<sup>92</sup>The term 'simple' applies to MacArthur and Wilson's graphical model. Their mathematical model is not simple at all.

births and deaths.



**Figure 11:** MacArthur and Wilson's equilibrium model. Where immigration rate (I) balances extinction rate (E), the number of species is in equilibrium ( $\hat{S}$ ) at a constant turnover rate  $\hat{R}$ .

MacArthur and Wilson present their theory graphically (figure 11) by plotting the immigration (I) and extinction (E) rates against the number of species (S) already present on an island (with a maximum number, P, equal to the number of species in the species pool on the mainland). They assume curved, concave relationships. They assume that the I-curve will be concave because, as an island is colonized, there will first be a fast and massive immigration of species with high dispersal abilities, leading to a strong decline in the overall immigration rate, followed by the later arrival of slower colonists which will cause the curve to decline more slowly to its asymptotic value of zero immigration (as an island becomes saturated, the chance of newly arriving individuals belonging to a new species decreases and goes to zero when all species are present). As to the E-curve, MacArthur and Wilson assume that as the number of species on an island increases a combination of two negative effects will occur: the increasing effect of decreasing population sizes and hence increasing chances of species becoming locally extinct, and an increasing effect of interspecific interferences (especially competition), also possibly decreasing population sizes. Because the two effects may reinforce each other, MacArthur and Wilson assume that the E-curve will also have a concave, almost exponential shape. At the point of intersection of the I-curve and the E-curve, the immigration rate equals the extinction rate, and hence there is a balance between the number of species immigrating and the number of species becoming extinct. At this point, therefore, the number of species is in equilibrium. The equilibrium number of species ( $\hat{S}$ ) is obtained by dropping a perpendicular from the point of intersection of the I-curve and the E-curve on the ordinate. The equilibrium is dynamic, because, though the number of species remains the same, the species composition may change continually. The rate at which this happens, called the equilibrational turnover rate ( $\hat{R}$ ), is obtained by dropping a perpendicular from the point of intersection of the I-curve and the E-curve on the abscissa. The turnover rate is constant, as soon as  $\hat{S}$  is reached.



**Figure 12:** Explanation of the distance effect (a) and the area effect (b) by MacArthur and Wilson's model; n = near, f = far, s = small, l = large.

As mentioned earlier, MacArthur and Wilson assume that the immigration rate depends only on the distance of an island to the mainland: the larger this distance, the lower the immigration rate. This means that the I-curve is lower for more isolated islands than for less isolated islands (figure 12a). The authors assume also that the extinction rate depends only on the area of an island: the larger an island, the lower the extinction rate. This means that the E-curve is lower for larger islands than for smaller islands (figure 12b).

With this simple model several predictions can be made:

- 1) The number of species at equilibrium is larger on near islands than on far islands (see figure 12a:  $\hat{S}_n$  is larger than  $\hat{S}_f$ ). This prediction is at the same time an explanation of the distance effect.
- 2) The turnover rate at equilibrium is lower on far islands than on near islands ( $\check{R}_f$  is smaller than  $\check{R}_n$ ).
- 3) The number of species at equilibrium is larger on large islands than on small islands (figure 12b:  $\hat{S}_l$  is larger than  $\hat{S}_s$ ). This prediction is at the same time an explanation of the area effect.
- 4) The turnover rate at equilibrium is higher on small islands than on large islands ( $\check{R}_s$  is larger than  $\check{R}_l$ ).
- 5) The decrease of  $\hat{S}$  with increasing distance (that is, the distance effect) is more pronounced on large islands than on small islands. This cannot easily be seen from the graphical model but follows from the mathematical version of the theory. The crucial factor is that the E-curve is lower for large islands than for small islands.
- 6) The increase of  $\hat{S}$  with increasing area (that is, the area effect) is more pronounced on far

islands than on near islands. This too follows from the mathematical model. The crucial factor in this case is that the I-curve is lower for far islands than for near islands.

Another, general prediction of MacArthur and Wilson's model is that the turnover rate at equilibrium, and hence the extinction rate at equilibrium, is much higher than one used to think. In their mathematical model, MacArthur and Wilson develop the following relation for the turnover rate:

$$\check{R} = 1.16 \hat{S}/t_{0,9}$$

where  $t_{0,9}$  is the time required to reach 90% of the equilibrium number of species (starting from  $S = 0$ ). Supposing, for example, that  $t_{0,9} = 50$  year and  $\hat{S} = 300$ , on average 7 species per year would become (locally) extinct!

### 12.2.3 Testing and evaluation of the model

A great many researchers have tried to find empirical support for MacArthur and Wilson's theory (hereafter: the M/W-model). Most of these studies consist of attempts to determine species-area relations and species-distance relations, and some of attempts to measure turnover rates. It appears from these studies that the M/W-model faces a number of serious problems.

In the first place it appears that although there is almost always a qualitative relation between species number and island area, there is no equivocal quantitative relation (Slud 1976; Connor & McCoy 1979; Gilbert 1980; Williamson 1981). The relation is different for different taxonomic groups and for different biogeographic regions and in almost all cases there is a large variation in species number per area class. That is, species-area relations turn out to be more often clouded than straight lines (or curves, depending on the scale one uses). In a review of the evidence on species-area relations for birds (a taxonomical group showing the best fit to a straight line) Slud (1976) concludes that "Insular biotas (...) conform to no universal standard and their compositions are each the unique result of an interplay among many factors that are differently peculiar to islands: this makes islands synecologically nonintercomparable" (in Gilbert 1980, p. 217). And Gilbert (1980, p. 220), who reviewed all the literature on species-area relations up to 1980, concludes: "It seems to me to be difficult to base a theory of the numbers of species on islands upon such evidence as is presented above, let alone one with such wide ramifications".

This problem seems to be less serious for species-distance relations, but these are considerably less well documented. Williamson (1981) notes, moreover, that it is very difficult in most cases to unravel the effect of distance on species number from all other characteristics in which islands may differ from one another (which is so much as saying that, apart from area, distance is not the only factor determining species number).

Another problem is that species-area relations can also be explained in terms of other factors than are assumed in the M/W-model. I have already mentioned the main alternative theory: larger islands generally contain more biotopes than do small islands, each with their complement of species. This means that species-area relations, even if they would be equivocal, in themselves do not provide evidence for the M/W-model (as has been assumed by many authors; see Gilbert 1980). The same applies to the distance effect. This can also be explained by simply assuming differences in dispersal abilities between species. Besides, isolated islands are often also small islands with a smaller biotope diversity, whence the

distance effect may also be the result of the biotope effect.

The conclusion to be drawn from this is that the area and distance effects can be tested properly only if other possible factors can be excluded or held constant. A biotope-independent area effect has been confirmed only by Simberloff (1976) and by Simberloff and Abele (1976), and was made plausible by Abbott (1978) and Lawton (1984). A biotope-independent distance effect has been confirmed only by Simberloff and Wilson (1969, 1970). On the other hand, there is innumerable evidence in favour of the biotope effect.

Another alternative theory is, moreover, that the number of species on islands may be determined also by the *evolution* of species. A particular aspect of this is *endemism*, that is, the occurrence of species (endemes) that are found only on a single island, or at most a group of nearby islands, and nowhere else. Endemism is most likely to occur on distant, isolated islands, as it requires the genetic isolation of species. Because it leads to an increase in the number of species, the effect of endemism runs counter to the distance effect and may complicate the latter considerably: on isolated islands the rate at which new species evolve may be equal to or even exceed the rate at which new species immigrate (Williamson 1981). On the other hand, endemism is most likely to occur on large islands, because of the lower probability of a new species population becoming extinct. Though this agrees with the M/W-model, it does mean that evolution of species may also be an alternative explanation for the species-area relation.

The crucial element of the M/W-model, in which it is distinct from other theories, is the prediction of an equilibrium in the number of species at constant turnover of species. Thus, it would seem that the best way to test the model is by testing this prediction. This has not been done often, however, probably because it is very difficult to establish at all whether something like stability or turnover of species occurs (see below). A general turnover of species has been confirmed only by Simberloff and Wilson (1969) and by Beven (1976, in Williamson 1981). The prediction that the turnover rate decreases with increasing distance, has been confirmed only by Simberloff and Wilson (1969, 1970). The prediction that the turnover rate increases with decreasing area, has been confirmed only by Diamond (1969) and by Jones and Diamond (1976). The results of these studies are controversial, moreover. Forced by criticism of the results of Simberloff and Wilson (1969, 1970), Simberloff (1976b) had to adjust the rate of turnover from 0.05 - 0.5 species a day to 1.5 species a year!

The chief problem with testing the M/W-model on this point is that it is very difficult to establish at all whether the number of species on an island is stable and whether a turnover of species occurs. In the first place the question is what is to count as 'stable'. How much variation in the number of species should one allow in order still to be able to talk of stability? How long is stable: ten years, twenty years, a hundred years? How is one to count all species? How many individuals of a species should there be in order for the species to be counted present? What to do with a species that is present one year and absent the next year? Depending on the scale of the system, studies of the stability of species number may be an extremely time-consuming, labour-intensive and costly matter. Naturally, such studies are scarce.

Another problem is well illustrated by the study of Simberloff and his colleagues. In order to demonstrate a biotope-independent area effect Simberloff (1976a) determined the number of arthropods on nine mangrove islands of different size. Because these islands all consist of only one mangrove species, they are equal in biotope diversity. Simberloff found a good relation between island area and species number. In a crucial experiment Simberloff and

Abele (1976) cut two islands into several pieces of different size and in time measured the number of species on the newly created islands. On all islands it stayed well below the number of species on the original (larger) islands. In order to demonstrate a biotope-independent distance effect Simberloff and Wilson (1969, 1970) first determined all arthropod species on various mangrove islands which had the same area but varied in distance to the coast. Next they defaunated the islands with methylbromide, a toxic substance which kills the fauna but leaves the vegetation intact. And then they counted the number of arthropod species (re)colonizing the islands in the following years, with the expected results. Perhaps experiments like this are the only way to really test ecological theories, but of course the cutting into pieces and defaunating of islands on a larger scale is practically impossible and ethically inadmissible.

Finally, the M/W-model has also been criticized on theoretical grounds. Thus, it has been argued that one of the crucial assumptions of the model, that the immigration rate depends only on distance, need not be correct. It may depend also on area: the larger an island, the larger a 'target' it is for potential colonists and hence the larger the chance of species being able to colonize (Simberloff 1976a; Williamson 1981). The assumption that the extinction rate depends only on area has also been criticized. Brown and Kodric-Brown (1977) have suggested that the extinction rate may be determined also by distance, because a population that is facing extinction may be 'rescued' by the immigration of new individuals of the same species, a probability which increases with decreasing distance. They call this the 'rescue effect'.

Yet another problem is that whether or not a species is successful in colonizing an island may be determined also by the presence (or absence) of other species. Species of higher trophic levels (herbivores, predators, parasites) will be able to colonize successfully only if species of lower trophic levels (plants, prey, hosts) are already present. (This can actually be seen as a component of the biotope effect, and more in particular as a resource effect, but trophic relations are usually distinguished from other biotope factors.) And the probability of successful colonization may be determined also by the presence of interspecific competitors, directly, through interference, or indirectly, through the exploitation of resources, both leading to smaller populations and hence increasing extinction chances. This would mean that the extinction rate depends not only on island area but also on the presence or absence of other species.

### **12.3            Reduction of the equilibrium model**

#### **12.3.1        Idealization and concretization**

After all these criticisms it is perhaps tempting to reject the M/W-model completely. However, this would do no justice to, first, the unifying value of the model, second, the great heuristic value which the model has had, and still has, for island biogeographic research, and third the fact that some supporting evidence for the model has been found. Even one of its strongest critics concludes that "The qualitative use of the equilibrium concept has stimulated a great deal of valuable research, and is clearly of use as a way of approaching an appropriate problem" (Gilbert 1980, p. 230). Also, although today the model is more or less left for what it is, it still forms the theoretical framework for discussing developments in island biogeography, and it is still presented in ecological handbooks as a major alternative (or, rather, complement) to the theories of biotope diversity and evolution of species on islands

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(see for example Begon et al. 1996; Krebs 1994). Thus, the conclusion should not be so much that the M/W-model has been rejected but rather that it has been insufficiently tested, and that it is difficult to test. There may be interference between area and distance, and underneath both concepts all kinds of factors may be hidden which, separately or in concert, determine the number of species on islands.

In more recent research the attention has shifted, therefore, from attempts to test or find evidence for the model towards causal analyses of the environmental factors on islands and the processes which determine not only the number of species but also their identity and hence the species composition of island communities (Brussaard 1984; Cohen 1989; Roughgarden 1989; Cody 1989; see below and the next chapter for examples). This agrees well with the account of developments in island biogeography provided by Haila and Järvinen (1980).

The core of the M/W-model is the equilibrium hypothesis. According to Haila and Järvinen (1980), this can be seen as a strict model, which either 'fits the facts' or not, but it can also be given a 'weaker' formulation. In this weaker formulation, one assumes that the probabilities of immigration and extinction depend only on the number of species and on the number of individuals per species. Both depend on area. From these premises also a dynamic equilibrium follows, but since the argument has now become deductive, the attention should not be focused on the equilibrium hypothesis but on the premises, that is, on the factors determining the rates of immigration and extinction. "Instead of testing (and potentially falsifying) the equilibrium hypothesis, this alternative formulation thus directs research towards ecologically significant factors" (Haila & Järvinen 1980, p. 268). As noted above, this is exactly what has happened in more recent research.

The question then becomes how to determine the processes of immigration (colonization) and extinction of separate populations are, and what mechanisms are important in different situations. Also, one must decide upon the level of explanation. "For example, colonization patterns have been studied both from a holistic and a reductionistic point of view (...); a good example of the community-level paradigm here is Diamond's (1975a and other papers) work on the colonization patterns of land birds in the archipelagoes surrounding New Guinea [emphasizing the importance of interspecific competition; see the next chapter; RL], while Järvinen and Haila [1984] interpreted colonization patterns of land birds in a Finnish archipelago on a reductionistic basis, in terms of the habitat requirements of individual species" (Haila & Järvinen 1980, p. 269).

According to Haila and Järvinen, there is no straightforward answer to the question whether there are general processes determining the structure of island communities or whether an idiographic (reductionistic) approach is more feasible. On the one hand it is clear that the M/W-model is too simple and too general as an explanation of the ecological characteristics of islands. On the other hand an idiographic approach alone is not sufficient either. Science doesn't consist of just collecting data, independent of theories and theoretical concepts. Without (implicit or explicit) theories, systematic observations are impossible and related problems remain unsolved. It is exactly this function which the M/W-model fulfilled.

Therefore, according to Haila and Järvinen, the developments in island biogeography with and after the introduction of the M/W-model can be described very well in terms of the model of idealization and concretization (Krajewski 1977; see also Nowak 1980; and chapter 3; see Tuomivaara 1994, on idealization in ecology). This model describes a process of growth of knowledge starting with an idealization step - the forming of a global theoretical concept or

model - followed by the stepwise concretization or factualization of this concept or model, leading to a better understanding of both its domain and its constraints. In the present example, the idealization is of course the M/W-model, and the concretizations are provided by the causal analyses of the ecological factors determining the processes of immigration and extinction of species. Though a separate role for island area and distance is still acknowledged, these concretizations involve a number of additional factors, the most important of which appear to be the biotope diversity on islands in relation to the environmental requirements and tolerances of species, the dispersal abilities of species in relation to island distance, and endemism. The extent to which interspecific competition is also important in structuring island communities is highly controversial (see the next chapter).

### 12.3.2 Co-operating research programmes

According to Gilbert (1980, p. 212), the M/W-model is distinct from the holistic traditions in ecology in the sense that it is based on the assumption that the number of species on islands is determined only by populational phenomena and ignores possible effects of interspecific competition.<sup>93</sup> Still, the model can be called a holistic model. Firstly, it is formulated at the level of communities. It is a model of the number of species, a main feature of the structure of communities. And although this is explained in terms of population phenomena (immigration and extinction of species populations), the variables of the model, immigration *rate* and extinction *rate*, are typically community variables. They cannot even be defined sensibly at the level of species (populations). Also, the *identity* of the species is left out of account (though of course in actual measurements of the number and turnover rate of species, the identity of the species must be established). Secondly, the model emphasizes an *equilibrium* in the number of species, a typical feature of holistic ecology (see 8.2.1), be it that MacArthur and Wilson assume no deterministic regulatory mechanisms responsible for the equilibrium, but stochastic processes.<sup>94</sup> Thirdly, as mentioned above, the term 'area' can be regarded as a sort of overall, umbrella term at the level of islands as a whole, underneath which all kinds of factors at the level of environments (biotopes), and matches between species and environments, may be hidden. In short, the model is typically directed at islands as wholes, and pays no attention to the component parts.

On the other hand, the more recent programmes in island biogeography, which are directed at the ecological factors determining the number and composition of species on islands, can be characterized as radically or moderately reductionistic, depending on whether they are more directed at, respectively, individual species and island characteristics (such as Haila & Järvinen 1984; see also the 'null' programme of Simberloff c.s. discussed in the next chapter) or interactions between species (for example Diamond 1975; Diamond & Case 1986; see the

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<sup>93</sup>This is not completely true, since MacArthur and Wilson assume that competition may reinforce the effect of decreasing population sizes with increasing species number, whence they give the extinction curve a concave, almost exponential form.

<sup>94</sup>This is an important difference, though. Holistic ecology is generally associated with determinism, and reductionistic ecology with probabilism (see, for example, Simberloff 1980; Kwa 1984, 1989; see also chapters 8 and 13).

next chapter).

It is obvious, therefore, that a link can be made between the model of idealization and concretization and the model of co-operating research programmes. As argued in chapter 3, idealization is more or less the same as approximation, and concretization is more or less the same as correction, which in turn is more or less the same as approximative reduction. Thus, the above-mentioned concretizations may also be seen as approximative reductions of the M/W-model. The M/W-model appears then as a holistic idealization which has played an important role as a guide programme for subsequent reductionistic programmes, and these latter programmes, in concretizing or reducing the M/W-model, appear as reductionistic supply programmes.

#### 12.4 Conclusions

The developments in island biogeography with and after the introduction of the M/W-model can be described very well in terms of the model of idealization and concretization. They can be described also in terms of the model of co-operating research programmes. The M/W-model may be seen as an idealization which subsequent programmes in island biogeography have concretized. In so doing, the model has acted as a holistic guide programme for these latter programmes which in turn, in concretizing or reducing the model, have acted as reductionistic supply programmes. Thus, the developments in island biogeography provide yet another example of the co-operation of holistic and reductionistic research programmes in ecology.

It is interesting to note, finally, that idealization and concretization are usually seen as a programme-internal development, that is, as a development *within* research programmes (Kuipers, personal communication). The present example makes clear, however, that it may also involve relations *between* research programmes. It seems likely that in these cases we are always dealing with programmes that are directed at different levels of organization, and, hence, with programmes that are in principle subject to the co-operation relation (as against competitive programmes which are generally directed at the same level of organization or domain). In these cases, it is also likely that the described process of growth of knowledge runs always from 'holistic' idealization to 'reductionistic' concretization. I cannot imagine what the reverse process, reductionistic idealization and holistic concretization, would be like.<sup>95</sup>

There is a major problem, however, with the above account. For according to the present reduction model, a reduction is the deductive or approximative derivation of the one law or theory by another, more general theory. That is, the model assumes that there is always one single theory acting as the reducing theory. In the above example, however, there does not seem to be one single reducing theory. Concretizations of the MacArthur/Wilson model involve several factors (and hence theories specifying those factors), which, in addition to island area and distance, may determine the number of species on islands: biotope diversity,

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<sup>95</sup>This is not to say that there can be no 'reductionistic' idealizations. All (deductive) reductions of idealizations are themselves also idealizations. See the example of the reduction of the Lotka/Volterra competition model to modern niche theory discussed in the preceding chapter.

habitat requirements of species, dispersal abilities, endemism, and interactions between species. Though in one concrete situation (one island or one archipelago) one factor may be predominant, and in another situation another factor, it seems that in general several of these factors act in concert (see the next chapter for an example). In fact, this may be the general pattern of reduction in ecology. If it is, there are two important consequences.

In the first place, with respect to the present example, it could mean that the reduction of the MacArthur/Wilson model is not a simple approximative homogeneous iso-reduction (see chapter 3), as presented above, but will turn out to be an example of approximative *heterogeneous micro*-reduction. For many of the factors involved in the concretizations of the model are micro-level factors (at the level of individual species and islands), as against the macro-level of the MacArthur/Wilson model. Unfortunately, it is too early yet to try and reconstruct the example in these terms (as the relevant research programmes are in active development).

In the second place, and generally, the consequence would be that there are several, more or less complementary and more or less equally important micro-theories acting together as reducing theories. This would be devastating to the idea of unification through theory reduction. I will return to this issue in the epilogue.