ISLAND BIOGEOGRAPHY – AN OVERVIEW

Scriptum

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Introduction

Various theories of island biogeography were developed in the past fifty years. These theories have been very inspiring for ecology in general, questions as to immigration, colonization of habitats and extinction are of basic interest. Most famous is the "equilibrium theory of island biogeography". As it is a rather simple approach the question occurs, what about the significance of the famous equilibrium theory? Is it really a trivial theory? Why is it so famous? Why is it an inspiring approach?

A first but rather preliminary answer can be derived from the history of ecology. The term ecology („Ökologie") was introduced by Ernst Haeckel in 1866, being an empirical science and a sub discipline of biology. His definition did not contain any research program, this was added by the Danish scientist Eugeniusz Warming in 1895, who was the founder of ecology as a „science"; for animal ecology this was added by Charles Elton („Animal Ecology", 1929). However, today, there are certain demands of modern philosophers of science: evaluation of theories and hypotheses, consistency of approaches, rigorousity of theories, strong reference to explanation (cause-effect-mechanisms), theory extension etc. Those aspects are met by the equilibrium theory of island biogeography.

History of science shows that scientific approaches were successful, when basic hypotheses and theories are expressed in quantitative terms. By this, they could be handled with mathematic techniques and, subsequently, better be confirmed or falsified. According to modern epistemology and philosophy of science it is necessary to express theories in quantitative terms, an *explicandum* becomes an *explicatum* only, when it is expressed in quantitative terms, i.e. when measurement is possible. Early ecology was dealing with sampling, ordering, classifying of objects. Theories from other scientific fields (evolutionary biology, geography) were adopted and transformed. Ecological theories and quantitative concepts in a stronger sense were not available. An important reason for the success of the equilibrium theory was the fact that it is an approach working with quantitative concepts allowing confirmation, falsification, explanation, and prediction.

What is ecology dealing with? A modern definition of ecology was given by Begon, Harper & Townsend (1986): Ecology deals with the description, explanation and prediction of the distribution of individuals, populations and communities in space and time. By this (1) it is specified that it is a scientific approach (empirism: description, explanation, and prediction), (2) levels of observation (individuals, populations, and communities) are fixed, and (3) a certain matter of interest is given: distribution of objects in space and time.

It was important for the further development that Haeckel introduced ecology as a subdiscipline of biology. The position of ecology within life sciences is contrary to physiology or anatomy an ideographical approach, and contrary to systematics a dynamical approach (see table 1)[1]. It means that originally in ecology the focus was on explanation and understanding of singularities and not on detection of general laws, – it was a matter of natural history, and the procedure is historiographic. In the course of time it was often tried to introduce quantitative terms in order to elaborate general scientific laws (and cause-effect-explanations) in ecology as well – with more or less success. Compared to other approaches the equilibrium theory was most successful in this respect.

Table 1: Nomothetic and idiographic approaches in biology.

Nomothetic approach **Focus: general aspects**	**Idiographic approach** **Focus: special aspects**	
Morphology, Anatomy Physiology	Systematics Ecology	**Statical approaches** **Dynamical approaches**
Generalization	**Historiography**	

[1] See: Rickert, H. 1926. Kulturwissenschaft und Naturwissenschaft. 7. Aufl. Reclam Stuttgart 1986 (Engl.: Science and history: A critique of positivist epistemology). Windelband, W. 1894. Geschichte und Naturwissenschaft. Straßburger Rektoratsrede (http://www.fh-augsburg.de/~harsch/germanica/Chronologie/19Jh/Windelband/win_rede.html).

Relative Distribution and Relative Abundance of Organisms

As to the presence of organisms of certain species we make two simple observations:

- Comparably, few species are widespread and are present in nearly all sites, and on the other hand, comparably, many species occur only in restricted habitats, as these species have certain requirements as to habitat conditions.
- Comparably, few species occur in very high abundances, while usually many species occur in small population densities or are singularly present.

The results of these observations are valid for various spatial and temporal scales. By this, you have to distinguish the relative distribution and the relative abundance of organisms of certain species. The first observation is described in the framework of the analysis of species-area relations, the second in the framework of the analysis of species-abundance relations (figure 3, note that the relations are not linear).

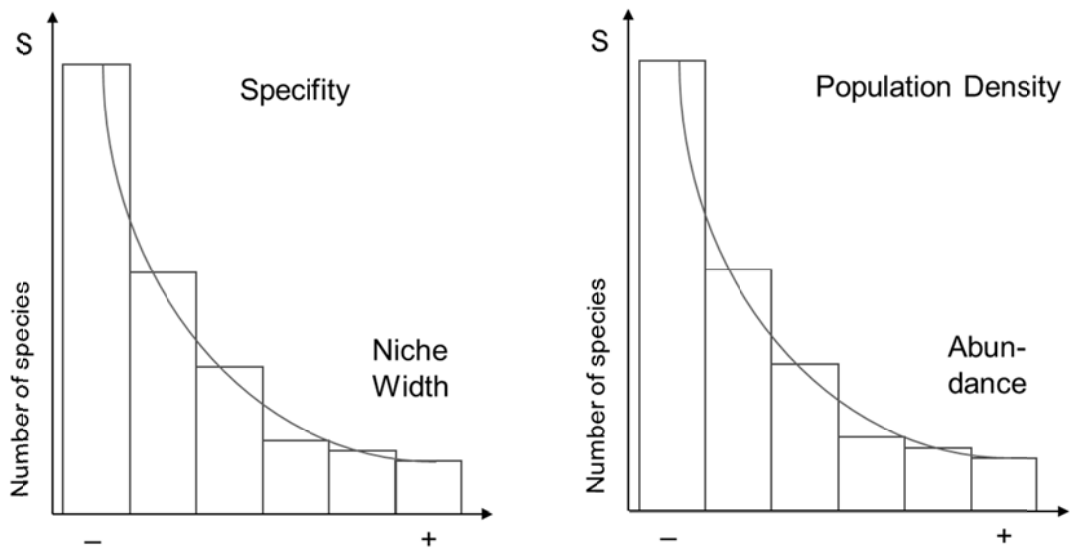

Figure 1: On species-abundance relations and species-area relations.

The Equilibrium-Theory of island biogeography was advanced based exactly on these two roots: The analysis of species-area relations (with either Arrhenius- or Gleason- plots) refers to the spatial and temporal distribution of populations; the analysis of species-abundance relations (with either rank-order or frequency plots) refers to the relative abundance of individuals within species assemblages. The equilibrium theory provides a combination of these two aspects.

Analysis of Species-Area Relations

Most often, the species-area relationships are analyzed with regression systems. It is assumed, that there is a close relationship between the area size (A) and the number of species (S), in some way, the larger the size, the higher the number of species. Two approaches have been evolved, the Arrhenius approach and the Gleason approach (see figure 2). Within the Arrhenius approach a significant linear relationship between log-

transformed area size and log-transformed species number it is assumed ("double log-transformation"):

$$S_{(A)} = c\ A^{z} \quad \text{or} \quad \ln [S_{(A)}] = k + z \ln(A) \text{ with } k = \ln(c) \text{ ["faunal coefficient"]}$$

Within the Gleason approach it is assumed that there is a significant linear relationship between log-transformed area size and the species number ("single log-transformation").

$$S_{(A)} = k + z * \ln(A)$$

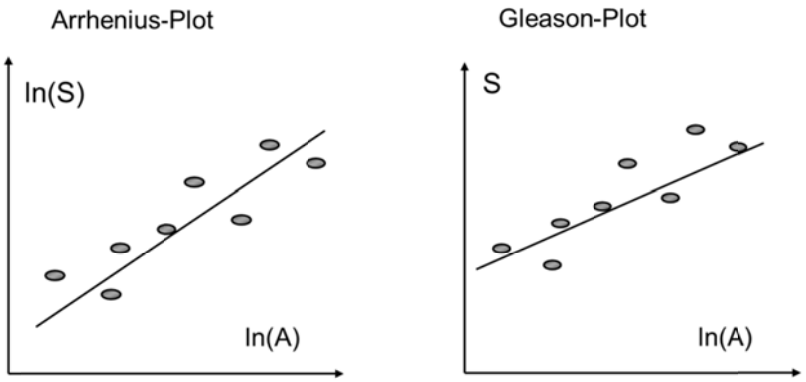

Figure 2: Arrhenius and Gleason plot: Relation between area size and species number.

The Darlington law was deduced according to empirical studies: twice the number of species when area size x 10 (that means that z in the first equation above is z = 0.301).[2]

Additionally it has been stated that the species number is increasing with time according to $S_{(t)} = c\ t^{z}$ which leads directly to the *area-per-se* postulate: species number depends on the area size exclusively.

Analysis of Species-Abundance Relations

In general, as to the species abundance relation the expectation is that comparably few species are very abundant, and comparably many species are rare. In order to express the species abundance relations in more detailed quantitative terms, several approaches have been advanced; three basic concepts are most important: the concept of the negative binomial distribution of species assemblages, the broken-stick distribution, and the (canonical) lognormal distribution.[3] The concept of the negative binomial distribution of species assemblages assumes that in natural communities the species abundance relation

[2] For details see: Arrhenius, O. 1917. Untersuchungen über Areal und Spezies. Svensk Bot. Tijdskr. 12: 180-188. – Gleason, H.A. 1922. On the relation between species and area. Ecology 63: 1643-1649. Darlington, P.J. 1957. Zoogeography. New York

[3] See in detail: Fisher, R.A., Corbet, A.S. & Williams, C.B. 1944. The relation between the number of species and the number of individuals in a random sample of an animal population. J. Anim. Ecol. 12: 42-58. – Preston, F.W. 1948 and 1962. The commonness and rarity of species. Ecology 29: 254-283. The canonical distribution of commonness and rarity, Part I. and II. Ecology 43: 185-215, 410-432. – MacArthur, R. 1960 and 1965. On the relative abundance of species. Am. Nat. 94: 25-36. Patterns of species diversity. Biol. Rev. 40: 510-533. – Williams, C.B. 1964. Patterns in the balance of nature and related problems. London.

follows a Poisson-distribution ("negative binomial"). This is the first "resource partitioning model" according to Fisher, Corbet & Williams (1944), it is presented most often as "rank-order plots" (figure 3, left). The model describes relative abundances of random samples often found in heterogeneous species assemblages with low species numbers or small collections, or under initial conditions with "scramble competition". The function is: $F_{(N)} = - \alpha \ln (\alpha N/N_{ges}) - c$ (with F = rank, N = abundance, c = Euler-constant, α = distribution variable). The diversity ("Shannon-entropy") can be calculated: $H_v = \ln (\alpha) + 0.557$.

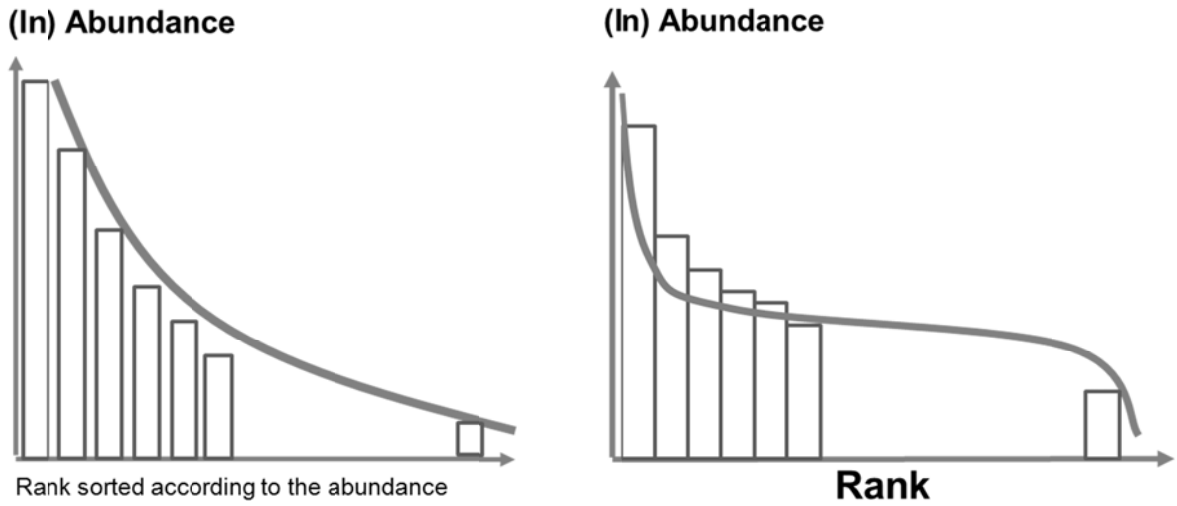

Figure 3: Rank-order plots for two natural communities: negative binomial distributed species assemblage (left) and broken-stick distributed species assemblage (right). Note the different shape of the resulting curves.

A differing resource partitioning model was advanced by MacArthur (1960). Here, it is assumed that the species abundance relation follows a "Broken-stick distribution" (figure 3, right), it is also presented as rank-order plot. In this model, "opportunistic" and "equilibrium species" are separated. The distribution is often found in mature communities, with a single ecological factor being dominant or dominant interspecific competition. The function is $F_{(N)} = S_{ges} * \exp (- S_{ges}*N/N_{ges})$, the diversity (Shannon-entropy) can be approximated with $H_v \sim= \ln (S_{ges}) – 0.42$.

Another representation of the species-abundance relations were proposed by Preston (1948, 1962). Species are classified in "octaves" according to the abundance in the sample: 1 Ind. → R = 1, 2-3 Ind. → R = 2, 4-7 Ind. → R = 3, 8-15 Ind. → R = 4, 16-31 Ind. → R = 5, 32-63 Ind. → R = 6 and so on. Note that it is a rough log-transformation to the basis 2. Frequencies are plotted as histograms (see figure 4). Within the approach it is assumed that species abundance in natural communities is lognormally distributed, and, moreover, canonically. This means that the species assemblage tents to the situation, that the octave of the most abundant species (R_{max}) is equal to the octave which represents the mean of the individuum curve (R_n): Preston introduced the term γ, $\gamma = R_n/R_{max}$, in the case of canonic lognormal distribution $\gamma = R_n/R_{max} = 1$.

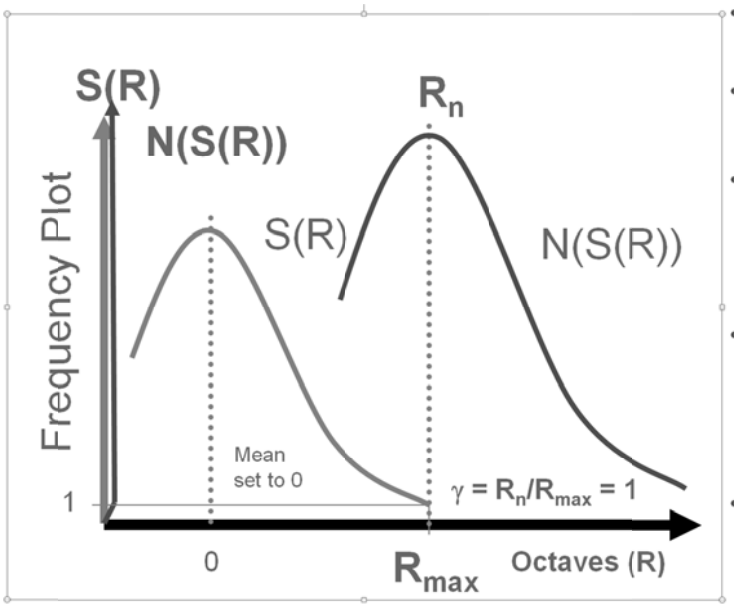

Figure 4: Canonical lognormal distribution of species abundance; frequency plot according to Preston (1948, 1962) (with R = octave, S = number of species, N = number of individuals, mean of the distribution transformed to 0).

Subsequently, it was shown that this type of distribution is often found in very heterogeneous species assemblages, with various abiotic factors dominant and various interspecific interactions. The calculation is according to $S_{(R)} = S_0 * \exp(-a^2 * R^2)$ with a = reciprocal value of the broadness of the distribution, S_0 = number of species in the modus of distribution, for which the curve shows his maximum; mean of the distribution transformed to 0. The diversity (Shannon-entropy) can be calculated for $\gamma = R_n/R_{max} = 1$: $H_v = \sqrt{(2 \ln(S_{ges})/p)}$. By negative integration of the species curve in the frequency plot the curve for the lognormal distribution can be plotted in the rank-order plot for comparison. The shape of the curves is different (figure 5).

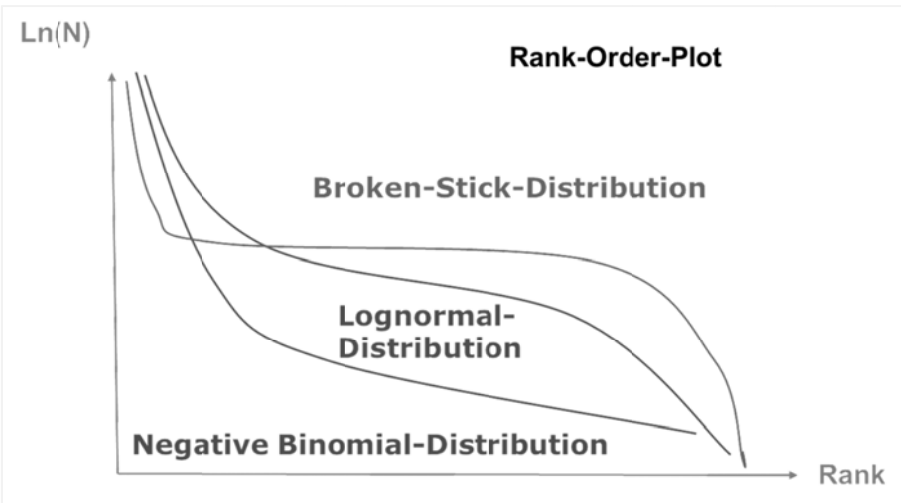

Figure 5: Comparison of different types of species abundance distribution in a rank order plot.

The Equilibrium Theory of Island Biogeography

Main Idea of the Approach

The equilibrium theory of island biogeography was established by the two American scientists Robert H. MacArthur (1930-1972) and Edward O. Wilson (*1929). The basic preconditions MacArthur and Wilson found at the beginning of the 60th can be characterized by the state of discussion as to the species area and the species abundance relations:

- Formalization and quantification of the various approaches
- Linking models on species area and species abundance relations: The „fourth root law“
- Dynamization of theories by the analysis of immigration and extinction processes
- Formularization of the *area per se* – postulate

First, MacArthur and Wilson restricted their approach to islands, by this to isolated areas, because these environments have clear borders which make it easier to be studied. It has been important that Preston (1962) advanced the combination of the species-area and the species-abundance relations: The “fourth root law” stresses the case that a community on an island is canonically lognormal distributed ($\lambda = 1$). It is also claimed that the abundance of the smallest population is not related and the total number of individuals is proportional to the area size. Furthermore it is stated that the regression coefficient („slope“, „z“) in log-transformed species-area plots on islands is 0.25 (¼):

$$\ln [S_{(A)}] = b + \tfrac{1}{4} \ln [A] \quad \text{or} \quad S_{(A)} = c + A^{1/4}$$

There is an approximation: $z = 1/(4\,\lambda)$ for $\lambda > 1$ and $z = 1/(1+\lambda)^2$ for $\lambda < 1$. The constants c and b are often called „biological“ or „MacArthur constants“. Numerical approximations revealed z = 0.262 (Preston 1962: 191) and z = 0.263 (MacArthur & Wilson 1967)[4]. – An illustration of the fourth root law is given in figure 6.

Based on these considerations the equilibrium theory was advanced. The process of colonization is analyzed in general. It is stated that the island species number is increasing during the colonization process to a certain extent. However, there is no linear relation, but a logarithmic, and the process stops when the species number of the mainland colonization source is achieved. Subsequently, the development of island species numbers is analyzed in detail by a simple consideration as to the immigration and extinction dynamics in the course of the colonization. Obviously, if species number on the island is small the immigration rate I (number of species arriving at the island within a time unit) is comparably higher, because the mean probability is higher that a new species colonize the island form the mainland source, while the extinction rate E (number of species going extinct within a time unit) is comparably small: few species, few extinctions. On the other hand, if species

[4] The basic studies: Preston, F.W. 1962. The canonical distribution of commonness and rarity, Part I. and II. Ecology 43 (2,3) 185-215, 410-432. – MacArthur, R.H. & Wilson, E.O. 1963. An equilibrium theory of insular zoogeography. Evolution 17: 373-387. – MacArthur, R.H. & Wilson, E.O. 1967. The theory of island biogeography. New York. – See also: Connor, E.F. & McCoy, E.D. 1979. The statistics and biology of the species-area relationship. Am. Nat. 113: 791-833. – Furthermore important: May, R.M. 1975. Patterns of species abundance and diversity. In: Cody, M.L. & Diamond, J.M. (eds.): Ecology and evolution of communities. Cambridge. – German readers may consult: Wissel, C. 1989. Theoretische Ökologie. Berlin.

number on the island is high, the immigration rate must be smaller (less species remain to colonize anew), while the extinction rate is higher (mean probability for a species to go extinct is higher if more species are present). In the equilibrium state which will be achieved in the course of time, both rates are equal: I = E and (theoretically) a constant species number is achieved (see figure 7).

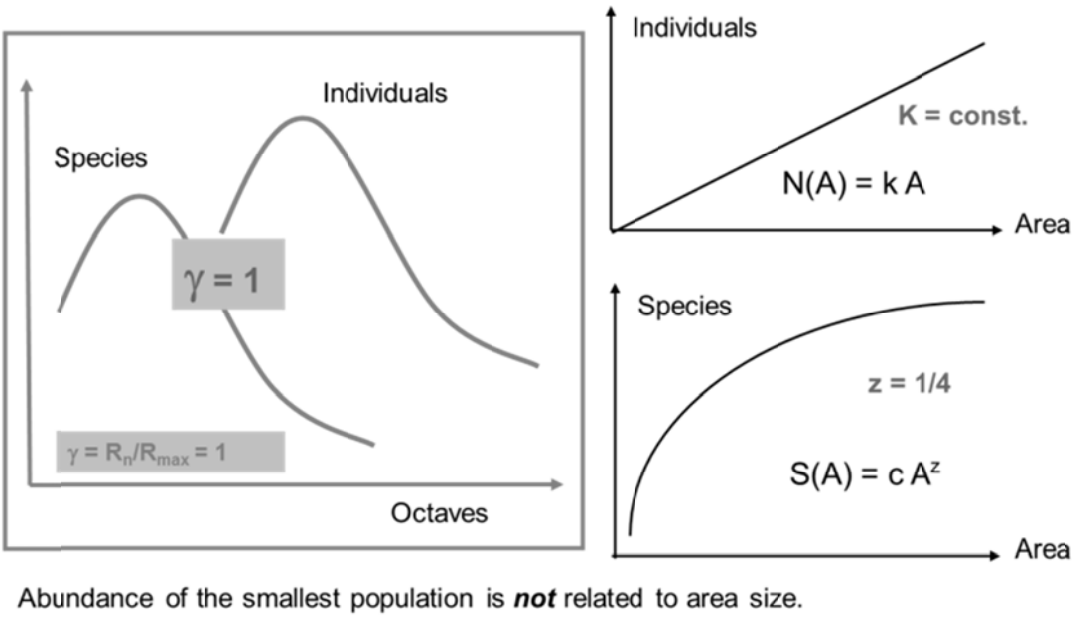

Figure 6: Illustration of the fourth root law.

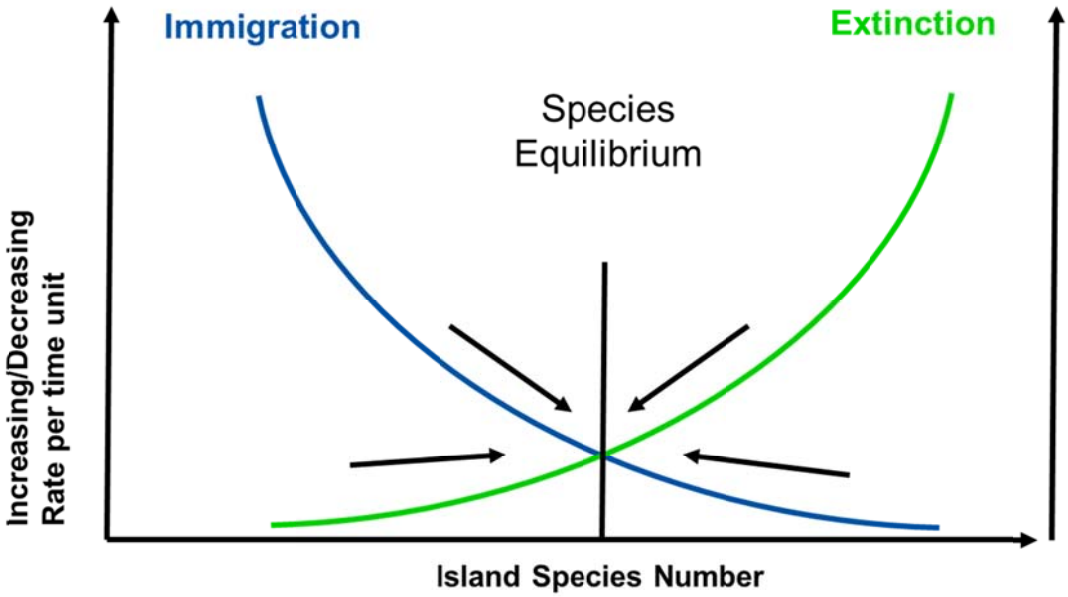

Figure 7: Immigration and extinction rates during the colonization process of an island. The equilibrium state is achieved when immigration and extinction rate is equal.

By the next step, the immigration rate and the extinction rate is analyzed. Obviously, the immigration rate mainly depends on the extent of isolation of the island, if the isolation is low (low distance to mainland colonization source) the immigration rate is comparably high. Secondly, it is assumed that the extinction rate depends on the area size: On large islands the mean probability is comparably lower that a species goes extinct, because it can avoid bad conditions. By this consideration the relations presented in figure 7 can be extended by defining various equilibrium states in relation to distance and area size as illustrated in figure 8.

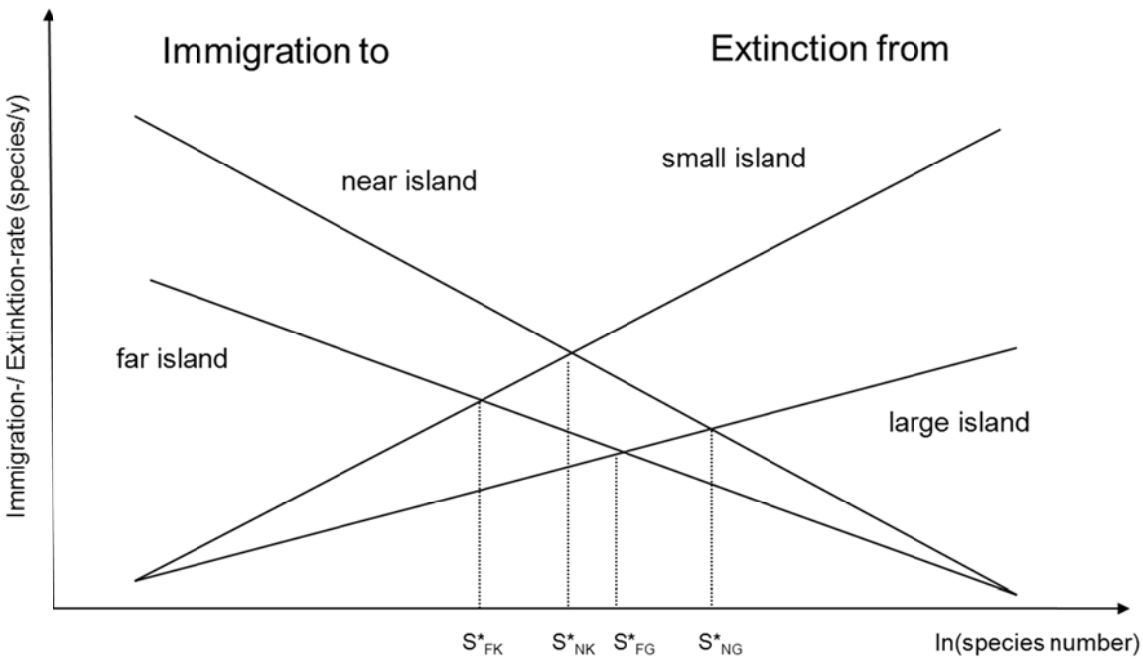

Figure 8: Immigration to and extinction on small vs. large and near vs. far islands, respectively.

Later, Diamond (1969)[5] defined the species-turnover for a specified intercensus interval which may be calculated by

$$Tr = 100 * (E + I) / (S_{t1} + S_{t2} - A)$$

(with E and I = number of emigrants and immigrants, S_{t1} and S_{t2} = total number of species at time t_1 and t_2, A = number of introduced species). In equilibrium state (number of species remain constant) you have (as previously shown) I = E. With $I = \mu (S_T - S)$ and $E = \lambda S$ you conclude $dS_{(t)}/dt = \mu S_T - (\lambda + \mu) S_{(t)}$, with λ and μ being the extinction and the immigration rate in time, and S_T the number of species of the source (mainland). After integration of the equation you find the number in which the system reaches equilibrium:

$$S^* = \mu S_T / (\lambda + \mu)$$

[5] Diamond, J. 1969. Avifaunal equilibria and species turnover rates on the Channel islands of California. Proc. Nat. Acad. Sci. 64: 57-63.

The equilibrium theory is also based on the "*area-per-se* postulate". Within this hypothesis it is stated that equilibration process exclusively depends on the island area size: Under the initial condition that the isolation of single islands of an island archipelago are of similar amount the number of species on the island exclusively depends on the island area size. In the case of canonical lognormal distribution the slope is z = 0.25 = ¼ (fourth root law).

There are several limitations of the theory more or less explicitly stated in the original publication:

- The equilibrium-theory exclusively refers to the species numbers. Population densities or special species compositions are not considered.
- The equilibrium-theory refers to island faunas in total exclusively. Proper results are to be expected only for similar (comparable) groups of organisms.
- The theory is purely calculatoric. Historical development of the islands is not taken into account. Especially evolution is not considered.

Immediately after publication of the equilibrium theory (MacArthur & Wilson 1963, 1967) various critiques and objections came up. The most important are:

- It is only mathematics, not biology that is reflected.
- Dispersion ability and possibilities to establish populations are not taken into account.
- Competition and further interspecific interactions are not taken into account.
- Special characteristics of insular habitats are not taken into account.
- Turnover calculations are dubious due both to „crypto turnover" (unrealized turnover within „census intervals") and „pseudo turnover" (turnover due to „transients").

On the other hand, the importance and significance of the equilibrium theory for ecological research (practically and theoretically) in general is evident.

- Elaboration of different extensions of the theory, which were inspiring for other fields of scientific ecology.
- Faculty of derivations of connections with and among other basic approaches and concepts in ecology which were extended themselves subsequently.
- Elaboration of interrelations of disparate concepts and theories, especially among biodiversity, species-area and species-abundance theory, which were separated before.
- Derivation of connections to practice in the field of applied ecology (nature conservation, „SLOSS", urban ecology).

Extensions and Applications

Since the publication of the equilibrium-theory in 1963, it was an object of violent controversy. On the one hand, several different approaches have been advanced, on the other hand, extensions and modifications of the original theory have been proposed. The literature dealing with problems of the equilibrium theory actually is hardly manageable.

Some extensions of the concept are[6]:

- „Interactive-“, „assortative-“, „evolutionary equilibration“ (Wilson 1969)
- Asymmetry between immigration and extinction rates (Brown & Kodric-Brown 1977): „Rescue effect“
- Turnover calculations considering different time intervals (Reed 1980)
- „Peninsular effect“ (Taylor 1987)
- Unified neutral theory of biodiversity and biogeography (UNTB) (Hubbell 2001).

The most influential contradicting approaches are the “habitat-heterogeneity theory” according to Williams (1964) and Lack (1969, 1975), and the “passive sampling“ approach according to Connor & McCoy (1979)[7].

Let us first briefly discuss two of the numerous extensions of the original approach which has been proposed by Wilson (1969) and Hubbell (2001). – Wilson (1969) suggested an extension of the equilibrium theory as to the development of different equilibration processes in the course of time (figure 9).

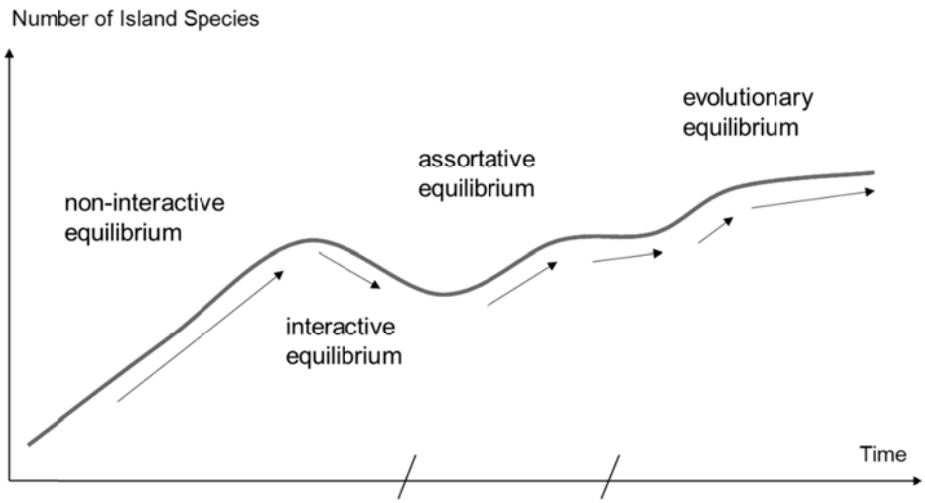

Figure 9: Different equilibration processes – non-interactive, assortative, interactive, and evolutionary equilibration according to Wilson (1969).

According to this approach, in the first phase a „non-interactive equilibrium“ species number will be achieved. All immigrating populations colonize the empty space. During the second phase the „interactive equilibrium“ will be achieved. Interspecific interactions

[6] See in detail: Wilson, E.O. 1969. The species equilibrium. Bookhaven Symp. Biol. 22: 38-47. Brown, J.H. & Kodric Brown, A. 1977. Turnover rates in insular biogeography. Ecology 58: 445-449. Reed, T.M. 1980. Turnover frequency in island birds. J. Biogeogr. 7: 329-335. Taylor, R.J. 1987. The geometry of colonization. 1. Islands. 2. Peninsulas. Oikos 48: 225-231, 232-237. Hubbell, S.P. 2001. The unifying neutral theory of biodiversity and biogeography. Princton University Press.

[7] Williams, C.B. 1964. Patterns in the balance of nature and related problems. London. Lack, D. 1969. The number of bird species on islands. Bird study 16: 193-209. Lack, D. 1975. Island biology illustrated by the land birds of Jamaica. Oxford. Connor, E.F. & McCoy, E.D. 1979. The statistics and biology of the species-area relationship. Am. Nat. 113: 791-833.

(competition!) lead to the decrease of the equilibrium species number. Subsequently, in the third phase „assortative equilibrium“ will be achieved: „even after species number equilibrium is reached, an `assortative´ equilibration process occurs as more highly co-adapted species sets find themselves by chance on an island and persits longer as sets“ (Simberloff 1976)[8]. In the course of the fourth phase „evolutionary equilibrium“ will be reached as speciation leads to an increase of the equilibrium species number again.

Another extension has been proposed by Hubbell (2001). The “unified neutral theory of biodiversity and biogeography” ("UNTB") was advanced based on the *area-per-se* – postulate, the results of the quantitative analysis of the species abundance relation and the equilibrium theory of island biogeography. The theory explains generation and development of biodiversity and temporal variation of relative abundance of species within communities and assumes that the differences between members of a community of trophically similar populations of species are “neutral”, that means irrelevant for their survival and success.

The interconnections and crosscutting topics among biodiversity, species-area- and species-abundance-relations with the linking concepts are illustrated in figure 10.

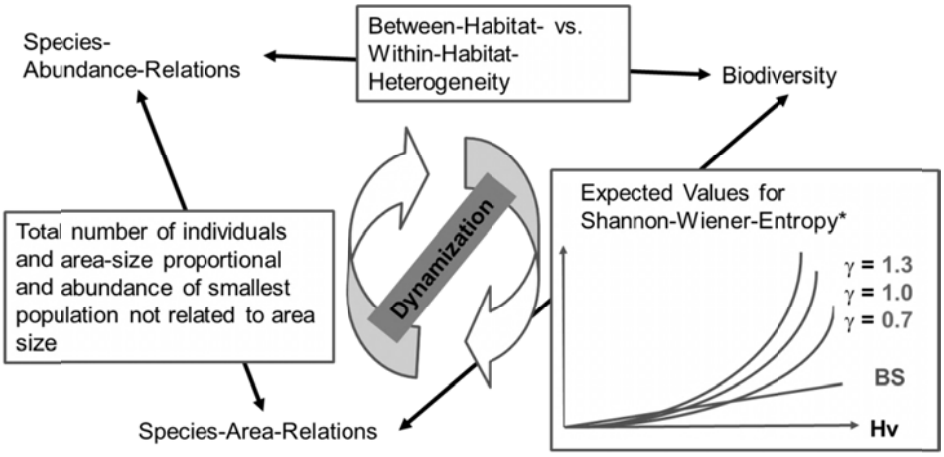

Figure 10: Linking biodiversity, species-area, and species-abundance relations (* according to May in Cody & Diamond 1975).

Beside the various extensions many connections with different fields of general ecology have been advanced. Examples are:

- Relation to different approaches in population ecology. – The separation of „opportunistic“ and „equilibrium species“ within the equilibrium theory is related to the constants K (space capacity) and r (mean reproduction rate) from the Lotka-Volterra differential equations, i.e. modifications of $dN/dt = r \times N ((K - N) / K)$. By this, the r- and K-strategy (r- and K-selection) approach is advanced.

[8] Simberloff, D. 1976. Species turnover and equilibrium island biogeography. Science 194: 572-578.

- Relation to succession and disturbance theory. – Simulation models of the variation of landscapes diversity on islands were advanced; it was shown, that succession related to certain disturbance regimes depends on the island area size, larger islands have more constant habitat heterogeneity, and species area slopes depend on the species number of the mainland species pool. By application of Markov-chains turnover process in the course of island colonization were simulated in order to receive reliable predictions.

Applications

Several applications of the equilibrium theory for practical conservation issues have been discussed.[9] Two examples are given.

Single Large or Several Small ("SLOSS")

About 10 years after publication of the equilibrium theory the discussion on „SLOSS" as to an optimal nature reserve design came up repeatedly. It was discussed, whether nature reserves should have a minimum area size, and whether it is more appropriate to have single large or several small nature reserves under limited conditions.

Proponents of the equilibrium theory admitted in a quite early stage of the discussion, that the MacArthur/Wilson concept does not necessarily lead to an optimal design of nature reserves. However, many ecologists and nature conservationists tried it again and again. – Additionally and subsequently, different concepts as to „minimum viable population" (MVP, 50/500 rule, etc.) were advanced[10].

Urban Ecology

Beside isolated nature reserves (see SLOSS discussion) isolated biotopes in urban areas were investigated as to the applicability of the equilibrium theory. It was assumed that the variation of species number can be analyzed and predicted with the equilibrium theory, for instance in order to argue for the importance of nature conservation in urban areas.

Immediately after popularization of the equilibrium theory the applicability of the concept as to isolated environments of inland areas (e.g. parks in cities) were discussed, although MacArthur & Wilson (1963: 386) wanted to restrict the concept to the avifauna of Indo-Australia exclusively. Soon, evidence could be given that equilibrium theory cannot be applied to inland situations without any additional considerations. The reason might be that the isolation of inland areas is low compared to the migration ability of the organisms to colonize. However, a limited and careful application as to invertebrates may be possible.

Summarizing Some Aspects

The equilibrium theory of island biogeography is a milestone in the history of ecology. This is due to its inspiring power over decades; numerous ecologists discussed, and

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[9] German readers may check also: Mader, H.-J. 1980. Die Verinselung der Landschaft aus tierökologischer Sicht. Natur u. Landschaft 55: 91-96.

[10] See papers in Soulé, M.E. (ed.) 1987. Minimum Viable Populations for Conservation. Cambridge.

elaborated the theory and related it to other scientific approaches in ecology. The theory is a rather simple but effective approach to analyze species-environment relations, and still a valuable approach to provide quantitative terms in order to elaborate scientific theory in ecology. The approach was shown to be rather capable as to distension and extension, and offered multiple connections to different scientific approaches and theories. Significant was the integration and synthetization of different and important approaches and theories dealing with analysis of distribution and abundance of species, which was essentially constitutional for ecology as a science since the beginning of ecological research.

Contradicting Approaches

Habitat-Heterogeneity Theory

The „habitat-heterogeneity theory“ was elaborated based on studies of Williams (1964) (dealing with plants), Lack (1969, 1976) (dealing with birds), and others as to colonization dynamics. It was intended to be a counter draft to the equilibrium theory according to Preston (1962) and MacArthur & Wilson (1963, 1967).

In a first step, it is admitted that there is a basic set of species on islands (theoretical number of species), which is approximated in the course of island colonization. However, it is not the island area size which is important for the amount of island species number, but the habitat heterogeneity of the environment on the island in total. Significant correlation between the number of species and the size of the island area are due to the fact, that most probably there are more different biotopes on larger islands and, by this, more ecological niches, which can be used by more different species.

Subsequently, numerous empirical confirmations were found that competition, resource partitioning as well as migration and dispersion abilities of colonizing species, respectively, and other effects are most important for the amount of species number on islands. The „habitat-heterogeneity theory“ is an approach that includes biological information in order to explain island colonization process. This is done by referring to environmental properties of the island environment and the ecological properties (niche width, dispersion ability etc.) of the colonizing species.

The number of species and the species composition („species assemblages“) is related to the „between habitat heterogeneity“ approach, however, it was turned out to be extremely difficult to express in quantitative terms (measurement). This is due to the fact that according to the multifunctional niche approach various properties of the environment (the landscape) must be considered. Most often, simply the number of different habitats present on the colonized island is used. Sometimes difficult „neighborhood coefficients“ after raster scanning of habitats are calculated, or calculations of environmental diversity according to Shannon-Wiener or Simpson‘s index. – „Within habitat heterogeneity“ is separated from „between habitat heterogeneity“. Within habitat heterogeneity includes the total heterogeneity of single habitats; frequently, measurement is based on the number of plant species occurring within the habitat.

Of course, adherents of the MacArthur-Wilson theory prefer within habitat heterogeneity in order to explain island species number with the explaining variable „number of plant species“, because island colonization by plant species itself must also be explained by area

size and the equilibrium theory, respectively. According to habitat heterogeneity theory, of course, between habitat heterogeneity is most important.

Many empirical studies have been carried out in order to give evidence for one of the two theories. It is not definitively solved; however, many examples have been published where habitat heterogeneity theory was likely better to explain species numbers of islands – sometimes both approaches have shown to have explaining power in different respects.

Passive Sampling Hypothesis

Subsequently, the famous „passive-sampling hypothesis“ was expressed and developed by Connor & McCoy (1979) after analyzing numerous data sets as to island colonization, relation of species-area significance and variation of species numbers on islands, and after testing equilibrium- and habitat heterogeneity theory. The main idea is that according to this approach island colonization proceeds as passive accumulation of single individuals according to area size: the *a priori* probability that in the course of accumulation more individuals of more different species arrive is higher on larger islands. This and only this is the reason for the fact that you will find more species on larger islands, and therefore the pure statistical species area relation most often holds.

First, it is stated that the species area relation („*area-per-se* postulate“) is just a statistical artifact resulting from the evidence of the canonical lognormal distribution of species abundance within an assemblage: actually, there is a high *a priori* probability for such a species abundance relation, when both comparably large areas and large species assemblages are included, and many different interactions take place.

Subsequently, it is shown that the slope of ¼ (fourth root law) is just an artifact of the regression system. The intercept occurring within the regression model is an artifact as well, and both the slope and the intercept are biologically senseless.

Additionally, it is stated that in contradiction to the equilibrium theory the immigration rate is not exclusively dependent on the island distance to the mainland source.[11] It depends on the area size as well: the larger the island the higher the probability that individuals of a certain species arrive at the island and establish sustainable populations. As to the equilibrium theory and the species-area relation, respectively, it is concluded that „it is manifested by the degree of correlation between species number and area, not the slope and the intercept parameters“ (Connor & McCoy 1979).

Connor & McCoy (1979) tried to give evidence for a direct proportionality between immigration rate and island area size. Some results have shown that it is true; however, the discussion still proceeds. A further conclusion is that both *area-per-se*- within the equilibrium theory and habitat heterogeneityt heory are probably correct and are not in direct contradiction: each of the approaches give answers to different questions.

[11] Many papers on this subject, see for example: Lomolino, M.V. 1990. The target area hypothesis: the influence of island area on immigration rates of non-volant mammals. Oikos 57: 297-300.

The passive-sampling approach was extremely influential in the scientific discussion and still have many adherents (probably most of the nowadays ecologists), however, it was strongly criticized (see e.g. „Sugihara/Connor controversy“[12]). Today, many proponents of the approach recommend taking the *area-per-se* hypothesis as null-hypothesis against other approaches.

Examples and Case Studies

Examples from Studies on the East Frisian Islands (Northern Germany)

On eleven East Frisian Islands, situated in front of the north-west German wadden sea area, species composition of various arthropod groups was studied between 1980 and 1994. Heteroptera (true bugs), Auchenorrhyncha (leafhoppers), Hymenoptera Symphyta (saw flies) and some others were included, data on the species number of plants, habitat heterogeneity, and area size were available as well.[13]

For various taxonomical groups evidence could be given for s significant species area relation, however, for different taxonomical groups the strength of correlations differed. For the group of heteropteran bugs species area relation is very close, while species habitat-diversity relation is weaker (see figure 11). The regression slope was higher than the predicted ¼ or 0.262, respectively (z = 0.293).

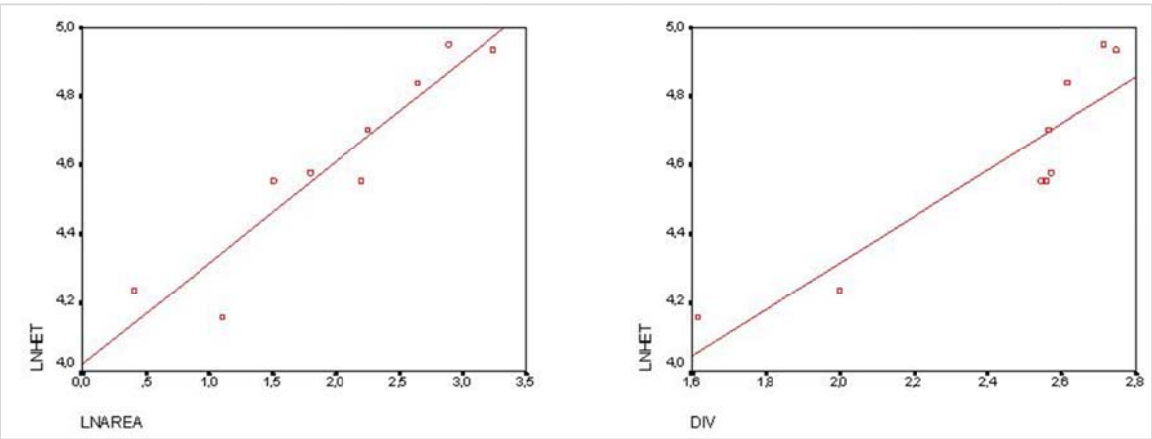

Figure 11: Species-area and species-diversity relations of Heteroptera (true bugs) on nine East Frisian Islands (linear regressions: number of species explained by area size, log-log plot with $r^2 = 0.939$, $p < 0.000$, $z = 0.293$; number of species explained by habitat heterogeneity with $r^2 = 0.903$, $p < 0.001$; taken form Bröring 1991, modified).

[12] Sugihara, G. 1981. $S = c A^Z$, z = ¼ : A reply to Connor and McCoy. Am. Nat. 117: 770-787. Connor, E.F., McCoy, E.D. & Cosby, B.J. 1983. Model discrimination and expected slope values in species-area studies. Am. Nat. 122: 789-796.

[13] The following data and analyses taken from: Bröring, U. 1991. Die Heteropteren der Ostfriesischen Inseln. Oldenburg. Niedringhaus, R. 1991. Strukturanalyse der Zikadenfauna der Ostfriesischen Inseln. Dissertation Universität Oldenburg. Oldenburg. Ritzau, C. 1995. Die Pflanzenwespen (Hymenoptera Symphyta) einer Küstenlandschaft am Beispiel der Ostfriesischen Inseln, Göttingen.

By this it is shown that species number of species of true bugs is related to area size to a huge extent: the larger the island the higher the number of species; and as the relation of species number to heterogeneity is significant as well: the higher the heterogeneity of the landscape, the higher the number of ecological niches, the higher the number of bug species. However, the relation of species number to area size is obviously higher, but in order to detect the combination of the most important factors and their relative contribution for higher species richness multivariate statistical analysis became necessary.

By multiple regression analysis a dependent variable is explained by more than one independent variable, here it is tested whether there is a multifunctional relation among different variables (table 2). First, simple correlations can be compared, the factors area size (log-transformed data: lnAREA) and diversity explain species number of true bugs (log-transformed data: lnHET) to a reasonable and significant extent; number of plant species (log-transformed: lnPLANT) is not significant. Interrelation among the explaining variables is high for the combination lnAREA/diversity and lnAREA/lnPLANT. These results can now be compared to the results of the multiple correlations analysis.

Table 2: Results of simple, multiple, and partial correlations among (log-transformed) number of species of true bugs (lnHET, variable to be explained), (log-transformed) area size, (log-transformed) number of plant species, and landscapes diversity on 9 East Frisian Islands (analysis with SPSS; * and ** = significant on p = 0.05 and p = 0.005 level, respectively; data taken from Bröring 1991).

Simple Correlation	**Coefficient (R)**	**Simple Correlation**	**Coefficient (R)**
lnHET-lnAREA:	0.822**	lnAREA-diversity:	0.635*
lnHET-lnPLANT:	0.422	lnAREA-lnPLANT:	0.683*
lnHET-diversity:	0.816**	lnPLANT-diversity:	0.181
Partial Correlation			**Multiple Correlation**
Impact	**Constant**	**r(lnS/E,k)**	**multiple R**
lnAREA	lnPLANT	0.6464	0.966**
lnPLANT	lnAREA	0.0717	
lnAREA	diversity	0.8470*	0.974**
diversity	lnAREA	0.7479*	

Multiple correlation is extremely high for the combination lnHET/lnAREA/lnPLANT (R = 0.966**), and for lnHET/lnAREA/diversity (R = 0.974**) as well. The best fit for species number of true bugs seems to be the combination lnAREA/diversity as the R-value is slightly higher. In order to detect the relative importance of single values in detail partial correlation coefficients are calculated: Partial correlation lnHET/lnAREA by exclusion of the impact of the number of plant species reduces the correlation coefficient from R =

0.966 to $r_{(lnHET/lnAREA,lnPLANT)}$ = 0.65, which is not significant any more, lnHET/lnPLANT by exclusion of the impact of the area size the reduction is much more significant ($r_{(lnHET/lnPLANT,lnAREA)}$ = 0.07). For this interpretation recall that lnAREA and lnPLANT is highly correlated. – Exclusion of diversity for the correlation of lnHET/lnAREA gives $r_{(lnHET/lnAREA,diversity)}$ = 0.84 which is slightly smaller than the multiple R, the impact of diversity is comparably low; exclusion of area size leads to a reasonable reduction of partial correlation coefficient to $r_{(lnHET/diversity,lnAREA)}$ = 0.75. By this it is evident: Most important is the area size. As a single parameter the diversity explains a high share of the variance of the species numbers as well, however, together with the area size the number of plant species is more significant. Thus, in this case the equilibrium theory holds throughout.

Different results were obtained for different groups of arthropods: correlation coefficients yield for all included groups significant results, thus, the species-area relation holds (best for true bugs). However, the slope is different; the expected slope of ¼ was never found. This is obviously due to the fact, the species-abundance is not canonical lognormal distributed on the island as expected as well. The reasons might be different, for true bugs it was shown, that the specific disturbance regime on the islands prevents the communities to become canonical lognormal distributed (Bröring 1991).

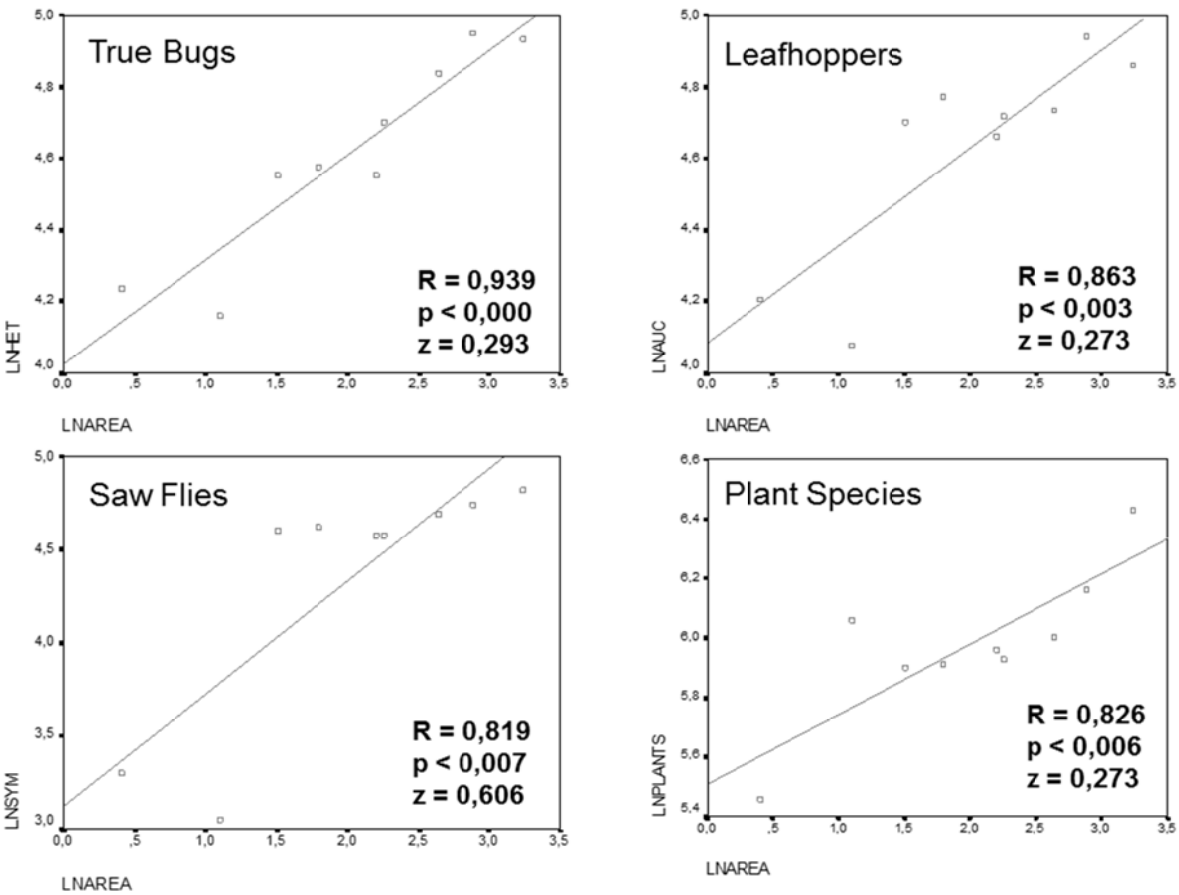

Figure 12: Results of regression analysis between species numbers of insect groups and area size of an island archipelago (nine East Friesian islands; all data log transformed).

Fresh- and brackish water bodies on these islands have also been studied as to species numbers of aquatic heteropteran bugs and the relation to different environmental parameters[14]. The situation of aquatic environments on the islands is different compared to terrestrial habitats, especially, because the isolation effect is twice: On the one hand, there is an isolation of single freshwater habitats from each other on an island. On the other hand, the island itself is isolated from the mainland colonization source. As to the species numbers the two questions arise in particular:

- What about the different number of species on different islands (table 3), the larger the island area size the higher the number of species?
- What about the different number of species on the level of single freshwater environments on certain islands (table 4), the larger the pond the higher the number of species?

Table 3: Results of regression analysis between numbers of species and area size for Nepomorpha (water bugs) and Gerromorpha (water striders).

Group	**S – log (A)**	**log (S) – log (A)**	
Nepomorpha	correlation = 0.811**	correlation = 0.832**	z = 0.224 p_z = 0.005
Gerromorpha	not significant	not significant	not significant

Table 4: Results of regression analysis between water bugs (Nepomorpha) and various environmental factors (N = number of aquatic environments included, log = log-transformed; ** = significant on 0.01 – level).

Nepomorpha (log)	Pearson	Spearman	N	Slope	Significance
Area size (log)	-0.33	0.08	207	-0.012	Not signif.
Salinity (log)	-0.353**	-0.351**	207	-0.135	0.000
Plant species (log)	0.292**	0.251**	154	0.300	0.000
Oxygen content	0.183**	0.216**	207	0.003	0.008
pH-Value	-0.179**	-0.219**	207	-0.117	0.010
Plant cover	-0.52	-0.040	117	-0.0005	Not signif.
Growing types (no.)	0.385**	0.377**	154	0.071	0.000

[14] Data according to Bröring, U. 2001. Analyse der Heteropterengemeinschaften von süßen und brackigen Gewässern auf küstennahen Düneninseln. Habilitationsschrift. Cottbus: 136pp. (available on the internet: http://www.tu-cottbus.de/fakultaet4/de/oekologie/lehrstuhl/mitarbeiterinnen.html).

Only for the group of Nepomorpha species number depends on the area size of the islands. The slope of the regression system is comparably low but highly significant. Species number of the aquatic environments is not significantly correlated with area size of the water body, nor with the extent of plant cover, but rather with factors like salinity, number of plant species, and diversity of plant growing types.

Case Study: Opencast Mining Area: Study Area and Study Sites

Investigations on the presence and abundance of various groups of species are carried out in the former brown coal mining areas of Brandenburg (Schlabendorf-Nord, Schlabendorf-Süd, Koyne/Plessa, Cottbus-Nord) in order to analyses the colonization process after dumping. Various open land habitats have been included: bare sand habitats, pioneer vegetation with ruderal herbs, short grass prairie with Corynephorus and xerophytic herbs, tall grass prairie with Calamagrostis, seeded grasslands, and heather. Regression analysis is applied in order to explain species number increase by time after dumping (figure 13, left). Canonical correspondence analysis was carried out in order to detect influences of different environmental parameters on animal community patterns including age (figure 13, right).[15]

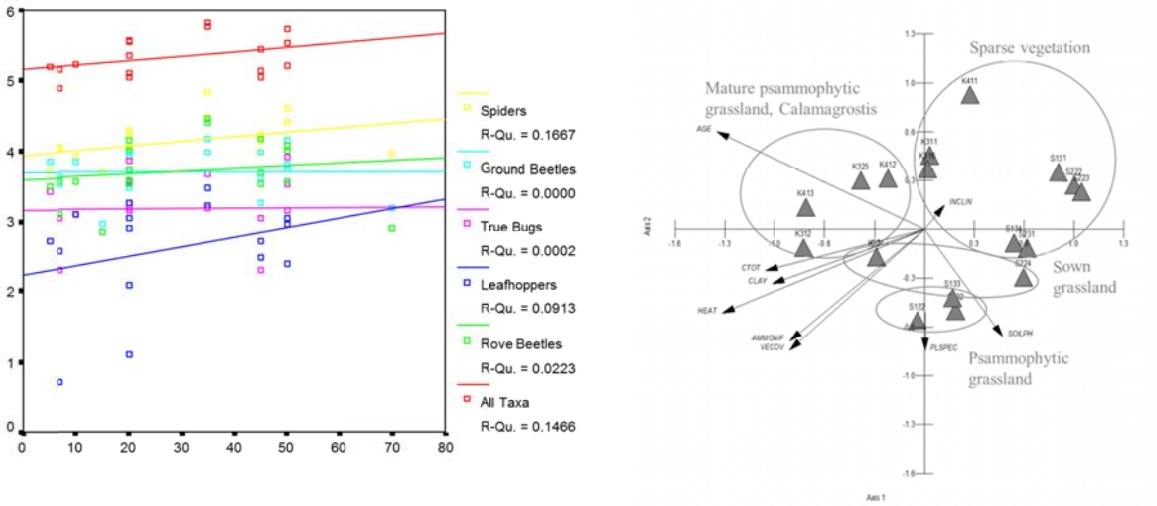

Figure 13: Results of regression analysis between species number and time after dumping for different groups of insects (left) and ordination diagram after canonical correspondence analysis based on 824 insect species, 17 investigated sites, and 9 parameters (right).

Contrary to the assumptions of the equilibrium theory it became evident that there is no constant species increase after dumping; none of the correlations were significant. On the other hand, with nine parameters including age 31.1 % of the variance of species abundances could be explained, different habitats are clearly separated due to certain animal community patterns. It remains unclear whether an equilibration process takes place.

[15] Taken from: Bröring, U., Mrzljak, J., Niedringhaus, R. & Wiegleb, G. 2005. Arthropod communities in open landscapes of former brown coal mining areas. Env. Ecol. 24: 121-133.

Conclusions

Summarizing Overview

Figure 13 provides a general overview of the roots for the formulation of the equilibrium theory of island biogeography and the effects: Generation of alternative approaches, various applications, elaboration of other theories, as well as modifications and extensions of the approach.

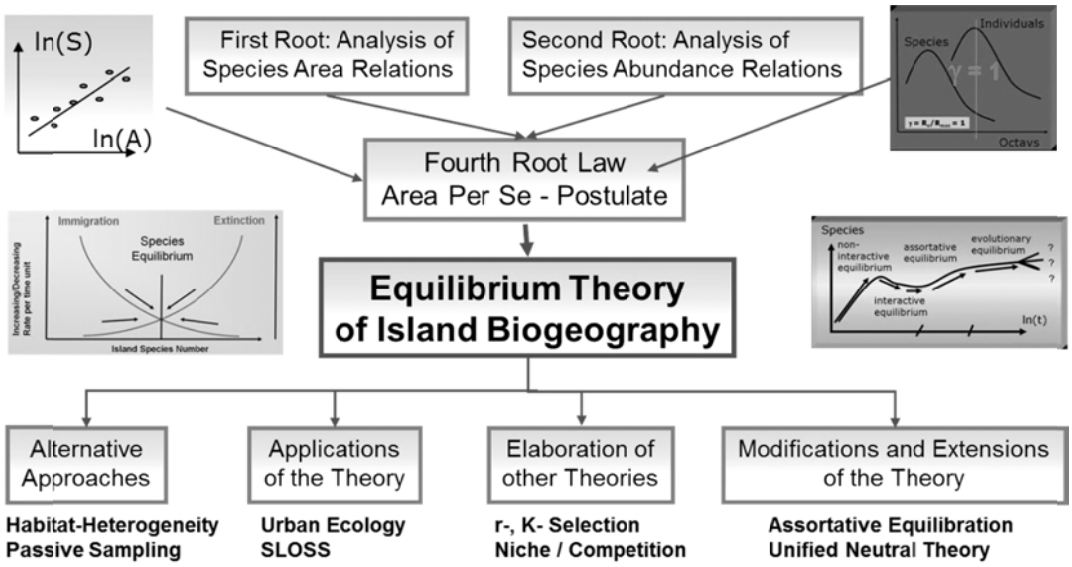

Figure 13: Equilibrium theory of island biogeography: summarizing overview including basic preconditions, contradicting approaches, applications, extensions, and modifications.

Outlook

After 50 years it is allowed to ask seriously: Is the equilibrium theory only of historical significance and importance for the analysis of developments in scientific ecology? There is evidence that work is continuing on the line. It is interesting indeed that a comparably simple idea has proven so effective, influential and stretchy.

Additional Literature

Begon, M., Townsend, C.R. & Harper, J.L. 2005. Ecology: From individuals to ecosystems. Blackwell, New York.

Gilbert, F. 1980. The equilibrium theory of island biogeography: Fact or Fiction? J. Biogeogr. 7: 209-235.

Krebs, C. & Hall, P. 2008. Ecology. The experimental analysis of distribution and abundance. 6th ed. New York.

Williamson, M. 1981. Island populations. Oxford.