האוניברסיטה העברית בירושלים
THE HEBREW UNIVERSITY OF JERUSALEM

THE EVOLUTIONARY ECOLOGY OF
SPECIES DIVERSITY IN STRESSED
AND EXTREME ENVIRONMENTS

by

DAN COHEN

מרכז לחקר הרציונליות

CENTER FOR THE STUDY
OF RATIONALITY

THE EVOLUTIONARY ECOLOGY OF SPECIES DIVERSITY IN STRESSED AND EXTREME ENVIRONMENTS.

DAN COHEN

Dept. of Evolution, Systematics and Ecology.
The Silberman Institute of Life Sciences. and
The Center for Rationality and Interactive Decisions
The Hebrew University of Jerusalem. Israel.
E-Mail: dancohen@vms.huji.ac.il

1. INTRODUCTION: THE DEFINITIONS OF STRESS AND EXTREME ENVIRONMENTS

1.1 THE ECO-PHYSIOLOGICAL DEFINITIONS OF STRESS IN PHYSIOLOGICAL AND ECOLOGICAL TIME SCALES.

A wide range of different definitions of <u>stress</u> conditions has been suggested. Some definitions deal mainly with the effects of extreme abiotic conditions (E.g. Oren, 1999). Other definitions are partly or completely circular, because the stress conditions are defined by the effect of low species diversity (E.g. Schink, 1999). Since most natural populations are limited in the long run by some combinations of limiting environmental factors, most species should therefore be considered to be stressed to about the same extent by the different limiting factors. (Chave, Muller-Landau, and Levin, 2002).

In this short essay I suggest that all stresses or extreme conditions should be defined as extreme levels of abiotic and biotic limiting factors <u>relative</u> to the distribution of the tolerance or utilization range of the dimensions or variables that define the habitats or the niche resources of the species. The ecological and physiological processes and conditions that determine the diversity of different types of coexisting species in different habitats and areas, for any <u>existing species' pools</u>, are reasonably well understood in principle. These processes and patterns will be discussed therefore only very briefly in this presentation.

1.2 THE DEFINITIONS OF STRESS OR EXTREME CONDITIONS IN EVOLUTIONARY TIME SCALE.

Such definitions are very problematic and difficult to realize. This is because the 'reference' normal utilization range distribution of the habitat resources or conditions utilised by the species, and/or the tolerance range of the niche dimensions of the species, can and do change in evolutionary time scales. The normal range may change by evolution in shifting environments, and/or by slow or fast evolutionary changes in many important features of the species. However, the mechanisms and constraints on the evolutionary changes of the normal range distribution of exploited habitat conditions or of the tolerance range within a species or lineage are still incompletely understood.

The normal range of habitat conditions or of the niche dimensions of species or lineages can be defined therefore only for relatively short-term evolutionary changes in the existing types of organisms, and may not exist for long-term evolutionary time scales. A proper definition of stress and extreme conditions relative to their normal range in evolutionary time scales is essential however for modeling and explaining the wide range of species diversity of different groups in different areas and habitats. (Rosenzweig 1995).

The evolutionary and ecological processes that determine the normal range of the habitat conditions exploited or tolerated by any particular lineage of species, usually change at very different rates for different types of organisms at different environmental conditions. These different time scales have to be taken into account in order to model and explain the existing and changing patterns of species diversity.

1.3 THE PATTERNS AND RATES OF SPECIATION

The patterns and rates of speciation of different types of species in different lineages and in different conditions and areas have a major influence on the numbers and types of species in the species pools of different ecological types. The conditions and processes that determine or influence the rates and directions of the formation of new species are only partly understood however, but they have a major influence on the different levels of diversity of different types of species at different habitats and conditions. (E.g. Rosenzweig 1995).

2.   MODELS OF SPECIES DIVERSITY

A number of different ecological, genetical, and evolutionary models and explanations have been suggested for the very wide range of species diversity of different types of organisms in different areas and environments. (E.g. Simberloff and Dayan 1991, Zobel 1992, Tilman and Pacala 1993, Iwasa et al 1993, Bengtsson, Fagerstrom, and Rydin 1994, Rosenzweig 1995, Chesson 2000, Chave, Muller-Landau, and Levin 2002,). As noted above, it is important to distinguish between processes that operate at ecological time scales and processes that operate at evolutionary time scales, and between local and geographical spatial scales.

2.1 ECOLOGICAL EQUILIBRIUM MODELS OF SPECIES DIVERSITY IN COMMUNITY ECOLOGY.

Ecological models of the conditions for the stable equilibrium coexistence of competing species that utilize an overlapping range of limiting resources have been extensively developed and analysed for a wide range of variation of stable and varying environmental conditions. (E.g. Pacala and Tilman 1994, Chesson 2000, Huntley and Chesson 1997).

  Some form of constant or shifting <u>resource partitioning</u> appears to be an essential component in all the models and experiments of the conditions that allow a long term <u>stable coexistence</u> of competing species, while also taking into account all the relevant spatial and temporal scales of the variations in the environment. (Cohen 1994, Huntley and Chesson 1997, Kinzig et al 1999, Chesson 2000).
According to such ecological models, the stable equilibrium of coexisting species from any given pool of species that compete for the same distribution of limiting resources, depends to a large extent on the degree of partition and specialization of the utilization of the available range of resources between the species. According to such models, the existing patterns of diversity and coexistence of competing species in different environments and ecosystems are maintained in approximate equilibrium in ecological time scales by the interactions between the ecological properties of the environment and the partition of resources by all the potentially available competing species. For example, a higher spatial <u>heterogeneity</u> of the environment in physical or resource space provides a larger number of opportunities for resource partitioning and for the coexistence of a higher diversity of specialized species. Higher <u>predictable temporal variability</u> of resources or conditions can also provide more opportunities for partitioning and specialization. On the other hand, <u>unpredictable</u>

variability in the environment favours the coexistence of a smaller number of generalist strategies of utilization of a wide range of resources under a wide range of conditions. Specific developmental and physiological constraints also restrict very strongly the possibilities for adaptive responses to extreme or unpredictable temporal changes. (Oren 1999).

The temporal and spatial scales of the variation and heterogeneity of the environment in an ecosystem are expected to influence the coexistence conditions of different species differently according to their ecology, mobility, and life history characteristics. (E.g. Chave, Muller-Landau, and Levin 2002). For example, long lived continuously active animals must feed all year around, and must therefore utilize a wide range of different resources that are available at different seasons and places. On the other hand, species that can become dormant and inactive for long periods may be able to maintain themselves by utilizing relatively rare specific temporary resources. Note however that the ecological models typically deal only with the conditions for coexistence of species from a given species pool. Note also that the evolution of the ecological characteristics of competing species that lead to higher or lower levels of specialization and diversity is still only very partly understood and ignored by most of these ecological models. (E.g. Zobel 1992, Tilman and Pacala 1993, Rosenzweig 1995).

2.2 NON-EQUILIBRIUM MODELS OF SPECIES DIVERSITY IN ECOLOGICAL TIME SCALES.

The coexisting competing species in any local ecosystem at any one time may very likely represent a ecological non-equilibrium. Clearly, the number and composition of species in any ecosystem at any one time represent the balance between the input of new species by immigration of new species from the existing species' pool in accessible areas, and by the formation of new species by speciation. The input of species is balanced by extinction of existing species at some probability, which decreases the number of species. (E.g. Hubbell 1979, Hubbel and Foster 1986, Chesson and Case 1986, Chave, Muller-Landau, and Levin 2002).

Ecological models of this type make explicit testable predictions about the effects of the spatial patterns of heterogeneity and of species mobility on the species diversity of different types of organisms in a wide range of different ecosystems in ecological time scales, for any given species' pool. The predictions of such island models have been tested and verified in a wide range of conditions. (E.g. Chesson and Case 1986).

The qualitative properties of non-equilibrium steady states of species diversity are similar however to some aspects of the equilibrium models. The probabilities or rates of extinction of species are influenced to a similar extent by the conditions that decrease the probability of coexistence in the equilibrium models. Similarly, the probabilities of establishment of immigrating or speciating new species are influenced to the same extent by the same conditions that increase the probability of coexistence in the equilibrium models.

However, such ecological non-equilibrium models also ignore the important long-term adaptive and non-adaptive genetic and evolutionary changes of the ecological properties and adaptations of all the species, which influence the probabilities for their coexistence. No less important is the lack of explicit modeling of the processes of genetic diversification within species and of the evolution of new species by speciation from existing species.

2.3   THE EVOLUTIONARY ECOLOGY OF SPECIATION

The genetical and ecological processes and conditions that determine the rates and levels of speciation have been investigated and modeled very extensively, but no consensus exists yet. (E.g. Rosenzweig 1995, Futuyma 1997) Many investigators have emphasized the genetical processes of speciation by the evolution of reproduction barriers between and within populations of the same species. One approach emphasizes the evolution of isolating mechanisms caused by the developmental or ecological low fitness of hybrids between differently adapted ecotypes, e.g. in host specialized herbivorous insects.
 A different approach emphasizes the evolution of isolating mechanisms by random drift or the random founder effect, or as a by-product of random differential selection in isolated populations of the species. Diversifying mate recognition behaviours and chromosomal rearrangements have also been suggested as important components in such processes of speciation. (E.g. Futuyma 1997).

2.4   SPECIATION IS PROMOTED BY SPECIFIC ECOLOGICAL ADAPTATIONS

Different local or specific ecological adaptations are expected to increase the probability of the formation and maintenance of ecologically and genetically distinct new species with different specifically adapted ecological characteristics. This is because hybrids between differently adapted parents are expected to have lower fitness than of each of the parents. On the other hand, strong unpredictable

fluctuations of environmental conditions are expected to have the opposite effect of strongly selecting against any local or habitat specific ecological specialization and genetic isolation. Frequent local random extinctions and re-colonization cause a similar effect of selection against the formation of specifically adapted new ecological or genetic types. Strong fluctuations of the selection regime that act on one or few major components of fitness, also decrease the fitness and select against the formation and establishment of different specific <u>epistatic</u> genotypic combinations. Such selection would reduce the stability of different adaptive peaks, and the probability for coexistence of a large ecological diversity of species.

Strong selection for a <u>single major</u> <u>fitness component</u>, even in a constant environment, is expected to decrease the number of distinct adaptive peaks, and thus acts to decrease the stable or steady state diversity of competing species in the ecosystem or community. See the model in Appendix A below. The low diversity of some types of species in some types of stressed and extreme environments and habitats may represent therefore the combined effects of a number of different ecological and evolutionary processes on species diversity in under such conditions.

3. MODELS AND MECHANISMS.

I suggest mechanisms that explain some of the general patterns in the processes and factors that decrease species diversity under some types of stress and extreme conditions.

3.1 BIOTIC STRESSES REDUCE SPECIES DIVERSITY LESS THAN ABIOTIC STRESSES IN BOTH ECOLOGICAL AND EVOLUTIONARY TIME SCALES.

This is because most <u>biotic</u> stresses, such as competition, predation, parasites, and diseases, cause mortality and other losses of fitness that are strongly <u>increasing</u> <u>functions</u> of the <u>densities</u> of the species in both ecological and evolutionary scales. Rare species are very much less likely to be a major component of the diet of any consumer species. Specific parasites and diseases are much less likely to cause high mortality in rare species. There is no or only very weak selective advantage for a common species to expand its niche to exploit the small range of partly negatively correlated resources exploited by any other coexisting rare species. The same arguments apply to diet choice by foraging animals, which tend to consume less of the rarer food organisms.

Both theoretical models and field data also strongly indicate that the <u>co-evolution</u> of predators, herbivores, parasites, and diseases with their biotically stressed <u>food</u> or <u>host species,</u> leads in many cases to <u>specialization</u> and <u>speciation</u> of a <u>higher diversity</u> and <u>coexistence</u> of both <u>stressed</u> and <u>stressor</u> species (Rosenzweig 1995). Such diversifying co-evolution may lead to high levels of species diversity in remarkably short evolutionary time of a few thousand generations. The species diversity may then increase more slowly or reach a steady state.

  Biotic stresses such as new predators, diseases, or strong competitors have caused the extinction of large numbers of species on many occasions during evolutionary history. However, most such biotic extinctions did not eliminate whole lineages, which may therefore recover and diversify quickly by new speciation under the new biotic stresses.

3.2   IN CONTRAST, ABIOTIC STRESSES STRONGLY DECREASE SPECIES DIVERSITY IN ECOLOGICAL AND EVOLUTIONARY TIME SCALES.

<u>Abiotic</u> stresses cause in most cases <u>density independent</u> mortality and other losses of fitness, which do not therefore reduce the probability of extinction as species become rare. In addition, rarity as such increases the probability of extinction of species by stochastic fluctuations in their population numbers or habitat conditions.

3.2.1 The effects of strong constant abiotic stresses.
Strong selection for adaptation to a major abiotic stress necessarily reduces the force of selection and the probability of existence of a large number of diverse genotypes with different adaptive specializations. This is because the total strength of selection on all fitness components in mutation-selection equilibrium is approximately constant. Thus, a very strong selection in any one major stress component necessarily reduces the strength of selection and the adaptive level of all other weaker components. (E.g. Kassen 2002). Also, even a weak negative trade-off between the fitness of specific specializations and the fitness of the major stress component would be selected against. The rare different types would not benefit by being rare, because the abiotic stress is also frequency independent. The number of different abiotic stresses is also very much smaller than the number of biotic stresses, so that the probability of evolving a large diversity of different specialized adaptations is necessarily also much smaller, and so is the expected realized diversity.

Metabolic, physiological, or ecological adaptations to extreme abiotic stresses may also require higher and increasing levels of energy expenditure for physiological and metabolic homeostasis and maintenance. This necessarily reduces the possible number and diversity of species with different viable <u>less efficient specialized adaptations</u> that can coexist or can evolve even under <u>constant stresses</u> in long term evolutionary time. Such a process has been documented in halophilic bacteria occurring in increasing salinity stresses. (Oren 2001).

3.4   A GENERAL MODEL OF THE OPPOSING EFFECTS OF BIOTIC AND ABIOTIC STRESSES ON SPECIES DIVERSITY.

I suggest therefore that a major fraction of the variance of the large scale global, geographical, historical, evolutionary, ecological, and physiological patterns of species diversity can be explained by the relative strengths of the <u>opposing effects</u> of <u>biotic</u> and <u>abiotic</u> stresses and limiting factors.

3.4.1 Stronger c*omplex biotic stresses increase species diversity*
The commonly occurring <u>biotic</u> stresses of predation, competition, parasites, and diseases, promote both the <u>coexistence</u> in ecological time scales of a higher diversity of species with <u>different specialized adaptations,</u> and the <u>co-evolution</u> of such a higher diversity of species with <u>different specialized adaptations</u> in evolutionary time scales. This would be the typical situation in species rich ecological communities, such as tropical rainforests and coral reefs, where biotic stresses dominate over abiotic stresses.

3.4.2 Stronger Abiotic stresses decrease species diversity.
Increasing levels of different types of <u>abiotic stresses,</u> such as extreme temperatures, salinity, drought, toxic materials, mechanical stresses of wind, currents, and moving sand, and of <u>local extinctions</u>, reduce the diversity and number of coexisting species from any potential species' pool in ecological time scale. <u>Abiotic stresses</u> also <u>select against</u> the evolution of a large diversity of specialized ecological or physiological adaptations and species in evolutionary time scales. This would be the typical situation in strongly stressed species-poor ecological communities, such as hot springs, high salinity waters, extreme cold, extreme drought, etc.

3.5 THE OPPOSING EFFECTS OF CONSTANT VS. CHANGING STRESSES.

The relative strengths of the two opposing processes of constant vs. changing stresses have already been identified as major causes for the different levels and patterns of species diversity. E.g. Chesson and Huntly 1997, Rosenzweig 1995, Tilman and Pacala 1993. Briefly, the arguments are:

3.5.1 <u>Constant</u> or <u>predictable</u> heterogeneous abiotic and biotic stresses at any environmental conditions and ecological communities allow the stable coexistence of a large diversity of species that are differentially adapted to different stresses and conditions. The same conditions of constant stresses in heterogeneous or predictable environments also select for the evolution of an increased diversity of high-fitness specialized adaptations that are better adapted for the particular stresses and conditions in the community.

3.5.2 In contrast, changing <u>unpredictable</u> biotic and abiotic stresses favour a <u>low diversity</u> of high-fitness <u>generalist</u> adaptations for a wide range of resources, habitats, and conditions in ecological time scale. Changing unpredictable stresses also provide a selective advantage in evolutionary time scales for a <u>low diversity</u> of species with high-fitness <u>generalist </u>adaptations for a wide range of resources, habitats, and conditions, in such changing unpredictable selection regimes.

3.6 DISCUSSION

In this short essay I suggest a very general model for the effects of two major processes that determine and explain the major trends of the effects of stresses on the patterns of species diversity:
1. The newly proposed concept of the differential effects of a small number of severe <u>abiotic</u> stresses that strongly <u>decrease</u> the diversity, as opposed to the effects of diverse <u>biotic</u> stresses that strongly <u>increase</u> the diversity.
2. The documented effects of the <u>predictability</u> and <u>constancy</u> of the ecological conditions and of the selection regime that increase the diversity vs. the effects of <u>change</u> and <u>unpredictability</u> that decrease the diversity. This general model that includes the combined effects of these two factors is compatible with the general patterns of species diversity in the world, and could explain a large fraction of the total variance of the distribution of the global patterns of species diversity. Additional appropriate scaling and normalization would probably be necessary to explain the details of the variations of species diversity in different types of

environments, functional ecological groups, or evolutionary lineages. Many of these differential effects could probably be incorporated as modifying components of the two main factors.

3.6.1 *Long term evolutionary and ecological changes in species diversity in different habitats and lineages during the history of the Earth.*

The long-term evolutionary expansion of the range of utilized resources and habitats during the history of the Earth by very many evolving lineages, probably began by an initial colonization of previously unexploited or unoccupied habitats or resources by very few colonizing species. Thus, such new habitats were by definition <u>stressful</u> initially for these colonizing species. Subsequent several stages of adaptive radiation by evolutionary and ecological diversification that occurred at later stages by the evolution of additional functionally adaptive specializations, then caused the existing rich patterns of species diversity.

3.7 CONCLUSIONS

Formulating and constructing a unifying framework for all the major processes and causes of species diversity, and especially the effects of stress and extreme conditions, is a major still unfinished task. The models in this essay, which emphasize the opposing effects of biotic vs. abiotic stresses and of constant vs. changing stresses, may provide some useful insights and ideas and some testable predictions. A large uncertainty still concerns the relative magnitude and appropriate scaling of the effects of different types of both biotic and abiotic stresses and of constant vs changing stresses on different types of organisms, and on the same organisms in different environments. Functional correlations and trade-offs between different types of adaptations are also difficult to include explicitly in the model without some specific assumptions.

   The proposed model necessarily leaves out many important issues and details. One major unexplained issue concerns the evolutionary constraints and costs of the evolution of different types and ranges of adaptations. The long-term evolutionary history of many different types of adaptations may provide us with some clues. For example, many types of adaptations have occurred independently many times in different lineages, suggesting that the evolution of such adaptations had to overcome only weak constraints. Other types of adaptations have occurred very infrequently or only once, suggesting that strong constraints have reduced the probability of their occurrence to extremely low levels. Large scale drastic

adaptations in evolutionary history have occurred most often under conditions of very strong stresses and directional selection and reduced competition, which could have provided the necessary conditions to overcome even strong constraints.

REFERENCES

Bengtsson J, Fagerstrom T, Rydin H. 1994. Competition and coexistence in plant communities. *Trends Ecol. Evol.* 9: 246–50

Chave, J., Muller- Landau, H.C. and Levin S. 2002. Comparing Classical Community Models: Theoretical Consequences for Patterns of Diversity. Am. Nat. 159, 1-23

Chesson P. 1994. Multispecies competition in variable environments. *Theor. Pop. Biol.* 45: 227–76

Chesson P. 2000. Mechanisms of Maintenance of Species Diversity. Ann. Rev. Ecol. Syst. 31, 343-66

Chesson P, and Huntly N. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Nat.* 150: 519–53

Chesson PL and TJ Case. 1986. Overview: Non-equilibrium community theories: chance, variability, history, and coexistence In *Community Ecolog*y, ed. J Diamond, TJ Case, pp. 229–39. New York: Harper & Row

Cohen, D. 1994. Modeling the coexistence of annual and perennial plants in temporally varying environments. Plant Species Biol. 9:1-10.

Futuyma DJ 1997 Evolutionary Biology. 3-rd Ed. Sinauer Associates .

Hubbell SP. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203: 1299–309

Hubbell SP. and R.B. Foster 1986. Biology, Chance, and History, and the Structure of Tropical Rain Forest Tree Communities: In Diamond J and T. J. Case. 1986. Community Ecology. Harper and Row. Pp. 314-330

Hubbel SP 1997. A unified theory of biogeography and relative species abundance, and its application to tropical rain forests and coral reefs. *Coral Reefs* 16: S9–S21

Iwasa Y, Sato K, Kakita M, Kubo T. 1993. Modeling biodiversity: latitudinal gradient of forest species diversity. In *Biodiversity and Ecosystem Functio*n, ed. E- D Schulze, HA Mooney, pp. 433–51. Berlin: Springer- Verlag

Kassen R, 2002, The experimental evolution of specialists, generalists, and the maintenance of diversityJ EVOL BIOL 15 (2): 173-190

Kinzig AP, Levin SA, Dushoff J, Pacala S. 1999. Limiting similarity, species packing, and system stability for hierarchical competition- colonization models. *Am. Nat.* 153: 371–83

Oren, A., 1999. Bioenergetic aspects of halophilism. Microbiol. Mol. Biol. Rev. 63: 334–348.

Oren, A., 2001. The bioenergetic basis for the decrease in metabolic diversity at increasing salt concentrations: implications for the functioning of salt lake ecosystems. *Hydrobiologia* 466: 61–72.

Pacala SW, Tilman D. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments *Am. Nat.* 143: 222–57.

Rosenzweig M. 1995. *Species Diversity in Space and Time.* Cambridge: Cambridge Univ. Press. 436 pp.

Schink, B., 1999. Habitats of Prokaryotes. In Lengeler, J. W., G. Drews & H. G. Schlegel (eds), Biology of the Prokarotes. Thieme, Stuttgart: 763–803.

Shmida A, Ellner S. 1984. Coexistence of plant species with similar niches. 58:29–55 *Vegetatio*

Simberloff D, Dayan T. 1991. The guild concept and the structure of ecological communities. *Ann. Rev. Ecol. Syst.* 22:115–43

Tilman D, Pacala S. 1993. The maintenance of species richness in plant communities. In *Species Diversity in Communities: Historical Ecological and Geographical Perspective*s, ed. D Schluter, RE Ricklefs pp. 13–25. Univ. Chicago Press

Zobel M. 1992. Plant species coexistence: The role of historical, evolutionary and ecological factors. *Oikos* 65: 314–20