

## **Relevant aspects of Ecological complexity and Evolutionary Ecology**

### **Natural history and ecology**

The relationship between ecology and natural history is central to one's conception of ecology as a science, and therefore to its practice. For example, in his attempt to make ecology more predictive, Peters (1991) tried to drive a huge wedge between the study of natural history and the science of ecology. He pointed out that the former is more of an art; the latter a science. Therefore, it can be concluded that they have little to do with each other. But this inference belies a major misunderstanding of how ecology has advanced at all, and how it can advance farther. While natural history and ecology may represent very different approaches, they share something extremely important: their subject. In fact, the art of natural history is more advanced than the science of ecology, and natural historians make more testable predictions than do theoreticians. There is much knowledge in the art of natural history, and one of the goals of ecological science is to transform this intuitive knowledge into scientific knowledge, and thus enable us to extend it. Using the craft of natural history, ecologists can create a wetland similar in most measurable ways to naturally occurring wetlands. There is a wealth of ecological knowledge, but most of it today is in the form of the craft of natural history rather than the science of ecology.

### **Pluralism in ecology**

According to the argument advanced here, ecology needs new ideas, approaches and theories. Thus, we need diversity and pluralism in ecological research. Abrahamson et al. (1989) have argued convincingly that ecologists should be more bold and open to new ideas, and less concerned about the dangers of fads. General theories of population dynamics, species diversity, etc., have not been very successful in generating testable hypotheses (Murdoch et al. 1992). The old debate about what limits population size, density-independent or density-dependent factors, assumes that population size is controlled by the same factors in all species in all communities.

Depending on the recent technological advances scientific research data are being collected from the on tracking individuals in the wild; ecosystem services rendered by the flora and fauna, or

remotely. mapping the habitats followed by proper analysis, inference, visualization, and explanation in respect of evolution of life-history, behavioural ecology (foraging and reproductive) and evolutionary ecology to understand the ability of individual organisms to maximize relative fitness.

**(a) Importance of Scales in ecobiological study :** Different biological processes operate over different scales and interact with different physical and chemical processes [116,117]; so ecosystem models require the application of scaling rules, both physical and ecological, from local and regional to global scales and across different levels of biological organization and processes (gene, individual, population, community, food webs and ecosystems) [28,95,97]. Developing models that resolve the appropriate physical, chemical, biological and social processes at different scales presents a major challenge [99,118-121], but scaling from individual behaviours to changes in population sizes at a regional scale is being attempted [100,122].

(b) Evolution Evolutionary change is also a ubiquitous feature of living systems. The extent to which it needs to be incorporated in ecological models will be determined by the relationship between the duration over which projections are made and the generation times of the organisms of interest. While models of forests typically run for periods equivalent to centuries or even millennia, the generation time of the trees will mean that only a small number of generations occur, and so evolutionary change during that time is assumed to be sufficiently small to be practically negligible.

**(b) Complexity Predictive systems ecology is 'big science'.**

It requires large amounts of data and complex models. To avoid the fate of classical systems ecology, model complexity must be decided carefully, and standardized approaches for describing individual organisms and their interactions and model structure are required. Just as big data analysis requires advanced computational statistics, predictive systems ecology will require models as complex as necessary to realistically represent ecosystems. In a complex system with multiple patterns, there may be trade-offs between agreement with different datasets or advantages in some cases to including particular processes that are not required for others. In such cases, a multi-model approach with replaceable components allows for different model purposes to be accommodated within an overarching scheme [58]. and is attractive from the

software development point of view, as it allows for flexibility in model development and implementation, so that different groups of specialists can develop their own component parts independently.

Complexity despite being inherent in understanding ecology as the product of its component parts, often remains untackled while researchers focus on simplifying systems to make them more tractable. Systems ecology will need to develop methods to deal with the availability of data - a significant advance could be made in ecology if more scientists working in the discipline adopted the habit of data sharing, and funders made free data access a condition for funding, as is the norm in some in other areas of science, and is being actively encouraged by funders in most countries.

### **Ecological complexity**

Complexity is understood as a large computational effort needed to piece together numerous interacting parts exceeding the iterative memory capacity of the human mind. Global patterns of biological diversity are complex. This biocomplexity stems from the interplay among ecological processes that operate and influence patterns at different scales that grade into each other, such as transitional areas or ecotones spanning landscapes. Complexity stems from the interplay among levels of biological organization as energy, and matter is integrated into larger units that superimpose onto the smaller parts. "What were wholes on one level become parts on a higher one." "Small scale patterns do not necessarily explain large scale phenomena, otherwise captured in the expression (coined by Aristotle) 'the sum is greater than the parts'.

**"Complexity in ecology is of at least six distinct types: spatial, temporal, structural, process, behavioral, and geometric." From these principles, ecologists** have identified emergent and self-organizing phenomena that operate at different environmental scales of influence, ranging from molecular to planetary, and these require different explanations at each integrative level. Ecological complexity relates to the dynamic resilience of ecosystems that transition to multiple shifting steady-states directed by random fluctuations of history. Long-term ecological studies provide important track records to better understand the complexity and resilience of ecosystems over longer temporal and broader spatial scales. These studies are managed by the **International Long Term Ecological Network (LTER)**.

## **Origin and establishment of the concept of Evolutionary Ecology**

The idea and concept of a sub-discipline "**evolutionary ecology**," has been conceived on deriving the merits of the subject ecology integrating some components of the subject population genetics, against physically stressful environments which include so many eco-evolutionary components such as evolution of life histories, mating systems, and sex ; the adaptability for territoriality, foraging , reproductive and social behaviors ; the theory of co-evolution and its application to adaptive radiation ,the species diversity of communities; the role of environmental heterogeneity in maintaining genetic variation In such context ,the development of the subject ecology as a self-conscious discipline assumed tremendous momentum in its development enjoying considerable autonomy throughout the first half of the twentieth century, experienced its conjunction with evolutionary biology in the 1960s .

This striking event was given much emphasis by the evolutionary ecologist especially in view of the fresh interpretation of Darwinian theory in the light of traditional taxonomy, paleontology , molecular biology and population genetics enjoying a separate line of evolutionary synthesis as the Neo-Darwinian synthesis during 1930s and 1940s. The impression that evolutionary ecology was marked vividly with works and messages of G. E. Hutchinson's and theoretical formulations of Robert MacArthur , Richard Levins', and G. C. Williams' urging of individual and genetic selection is the key to ecology's mysteries. The concepts put forward by James Collins and afterwards substantiated by W. C. Allee in 1949, strengthening the close bonding between ecology and evolution instead of dealing of either of the subjects separately. The late 1950s and the 1960s had also witnessed, a redirection in the fields of evolutionary ecology of a with its close ally, population biology to unravel the mystery of so many behavioral manifestations of animal kingdom.- Darwin's pioneering evolutionary synthesis based on theorizing ecological facts constituted integral structural elements to the evolutionary theory in interpreting the biogeography and its influence on flora and fauna.

The sub-discipline "**evolutionary ecology**," has been innunciated on deriving the merits and using the foundation of some "pure" ecology and some "pure" population genetics, which includes subjects such as the evolution of life histories, of mating systems, of sex; the

adaptability for territoriality and against physically stressful environments, foraging behavior, social behavior; the theory of co-evolution and its application to adaptive radiation, the species diversity of communities; the role of environmental heterogeneity in maintaining genetic variation

In such context, it can be argued that the development of the subject ecology as a self-conscious discipline enjoying considerable autonomy throughout the first half of the twentieth century, experienced its conjunction with evolutionary biology in the 1960s. This striking event was given much emphasis by the Eco-biologist especially in view of the forgers of the neo-Darwinian synthesis in the 1930s and 1940s which included geneticists, paleontologists, and systematists, but not ecologists especially because of the role of ecology in Darwin's work.

The impression that evolutionary ecology was marked vividly with works and messages of G. E. Hutchinson's and theoretical formulations of Robert MacArthur and Richard Levins', and with G. C. Williams' urging of individual and genic selection is the key to ecology's mysteries. The concepts put forward by James Collins and afterwards substantiated by W. C. Allee in 1949, strengthening the association between ecology and evolution having a long and varied history as that of either of the subjects considered separately. The late 1950s and the 1960s had witnessed, a redirection in the fields of Evolutionary ecology of a long-standing interaction with its close ally, population biology - Darwin's pioneering evolutionary synthesis based on theorizing ecological facts constituted integral structural elements to his evolutionary theory; the biogeography of Alfred Russel Wallace.

Much of early ecology was in essence a physiological approach to adaptation, and if the physiological ecologists were vague about mechanisms or skeptical of natural selection, they were none the less concerned with a central concept in evolutionary biology. They were naturalists, often more specifically ornithologists, entomologists, botanists, or ichthyologists, and in this role contributed to systematics, evolution, ecology, or behavior as the occasion arose or demanded

The attempt of some early ecologists to define ecology as distinct from evolutionary areas such as systematics and as directed toward the definition of phenomena and units of study that might be its special province. Sharon Kingsland and William Kimler in particular have discussed the

perceived need to acquire status for ecology as an autonomous, respectable science. In this regard some ecologists, as Joel Hagen has demonstrated, emphasized the need for rigor and turned toward the experimental sciences (particularly, William Coleman tells us, physiology) to achieve respectability, rejecting the speculation and imprecision that they thought on three aspects

**First** , The subject ecology along with evolution is intimately associated and inherent in taxonomy, phylogenetic analysis, historical biogeography, and natural history

**Second**, the core concept of Darwin's theory, natural selection, fell into disrepute for much of the early twentieth century. Taxonomists were of the opinion that differences among closely. Evolutionary ecology in its modern form, consisting as it does largely in adaptationist theory and test, could hardly exist until the climate of opinion about natural selection and adaptation had changed.

**Third**, ecology like most sciences underwent its own "adaptive radiation" into specialized niches such as limnology, phytosociology, biological control, and other applications. In many of these fields the major questions were and are functional rather than historical in nature; evolution and history need not be invoked if we wish to know what immediate factors govern the course of succession, the rate of phosphorus turnover, or the distribution of a species, given its physiology.

For many American ecologists of the 1950s and 1960s ecology was virtually defined by the content of Eugene Odum's *Fundamentals of Ecology*, the most recent edition of which contains in its index two references to evolution and none to natural selection, adaptation, or genetics.<sup>7</sup> Throughout this period, nevertheless, explicitly evolutionary currents run through ecology. As of 1964, J. Heslop-Harrison credited genecology with a history of forty years; Charles Elton had long discussed the possible genetic consequences of population fluctuations; Vito Volterra, Georgii Frantserich Gause, and Alexander John Nicholson had conceived their work, as Kingsland notes, in a Darwinian spirit; Allee and coworkers devoted 130 of the 730 pages of their *Principles of Animal Ecology* to "Evolution and Ecology"; and H. G. Andrewartha and L. C. Birch considered genetics explicitly in *The Distribution and Abundance of Animals*.

As Kimler notes in citing John Harper's definition of the subject, modern evolutionary ecology is in essence the analysis of the evolutionary origin of ecological phenomena with an explicit

recognition of the distinction among, and the consequences of, selection at various levels (gene, organism, kin group, population, or higher).

The new evolutionary ecology saw the hand of natural selection everywhere, recognized distinctions in level, and, most important, applied the concepts of individual selection and adaptation to properties of species - such as life history patterns - that had not been addressed before. The new evolutionary ecology, it appears, had several historical roots. Foremost among them is the legacy of the evolutionary synthesis: natural selection is not only real, it is powerful. R. A. Fisher, Sewall Wright, and J. B. S. Haldane had rescued natural selection in theory; Ernst Mayr, George Gaylord Simpson, Julian Huxley, G. Ledyard Stebbins, and others had found it compatible with the observations of systematists; Theodosius Dobzhansky, E. B. Ford, and their colleagues provided dynamic evidence.

The postsynthesis Darwin Centennial celebrations of 1959 forced biologists of virtually every field to pay homage to Darwin - and find his relevance to their particular disciplines.

Adaptation and Natural Selection, launched an era of individual-selectionist interpretation of life histories and behavior, topics that had been central in the arguments of Lack and Wynne-Edwards." Williams' appeal lay in his clear exposition of ecological issues in a genetic framework; the impact of Hutchinson, the polyhistor of ecology, lay perhaps in his extraordinary breadth of vision and his search for coherence in diversity.

and in his student Robert MacArthur the fulfillment of, the use of simple models that abstract the essence from the variety of the ecological world, recapturing Volterra's theory and pressing it into the service of new questions about the nature of communities. Although much of MacArthur's theory is an abstraction from pure population dynamics, questions about resource utilization and the coexistence of species rapidly and inevitably acquired an evolutionary dimension.

**Fourth**, as Collins has pointed out, there arose a recognition that ecological and evolutionary processes could be commensurate in time and space. This recognition came largely from the work of Dobzhansky and his collaborators and from the British ecological geneticists. It enabled ecologists to imagine experiments on genetic changes in the ecological relations of species, and

led Levins and others to argue that ecology could not ignore genetic processes, for the phenomena under study might evolve even as we watch

### **The present and future of evolutionary ecology**

Without doubt, a very considerable synthesis of ecology and evolutionary theory has occurred. On the theoretical front, both phenotypic and explicitly genetic models of coevolution, demographic properties, migration, niche breadth, and other population phenomena abound; and an empirical population ecologist is as likely as not to include some analysis of genetic variation in his or her work. The promise of an evolutionary theory of community structure has not yet been fulfilled; the currently debated issue in community ecology seems to be whether communities have any predictable structure at all. Ecosystems ecology, by and large, remains virtually uninfluenced by evolution. Perhaps evolutionary theory has little to say about energy flow and nitrogen cycles, but we do not even know if the primary productivity of a coevolved community of plants should differ from that of a random assemblage of species taken from around the world. Evolutionary questions posed at the community and ecosystem levels may prove to be unanswerable, but so far they have hardly been addressed. Evolutionary biology is made up of two major fields of study, between which there is far less communication than there should be: **the first one** deals with the analysis of evolutionary mechanisms and the second one is the inference of the history of evolution primarily developing the theory of evolutionary mechanisms that has been integrated with ecology.

### **Some examples of efficient theories**

Several deductive frameworks that fit our description of *efficient theory* have emerged in ecology and evolutionary ecology. In this section, we review and compare some of these theories to orient readers to key characteristics of deductive theory that we consider highly efficient and useful. From these comparisons, we argue that efficient theory in ecology is simple, parsimonious, derived from first principles, quantitative, and mathematical, with few inputs and many predictions.

**Fisher's sex ratio theory.** The argument behind Fisher's sex ratio theory is that the relative reproductive value to parents of sons (rather than daughters) is equal to the relative selection



pressure favoring the production of sons. Theory includes the assumption that parents determine the sex of their offspring and a definition of *reproductive value*. Fisher (1930) defined *reproductive value* in the context of populations with age structure, such that, given that an individual survives to age  $x$ , its expected reproduction from age  $x$  onward is  $v_x$ . This quantity is calculated in the discrete case as  $\sum_{y=x} l_y m_y / R$  and in the continuous case as  $\int_{y=x} l_y m_y dy / R$ , where  $l_x$  is the probability of surviving from age 0 to age  $x$ ,  $m_x$  is the average number of offspring produced by an individual of age  $x$  and  $R$  is the net reproductive rate of the population.

**Optimal foraging theory.** Optimal foraging theory (OFT) is concerned with understanding the decisions that individuals make while foraging in heterogeneous environments (e.g., MacArthur and Pianka 1966, Charnov 1976). OFT is intended to explain the foraging behavior of animals by means of a quantitative theory based on the first principles of energy and mass balance and natural selection. By assuming that natural selection has molded the behavior of organisms so as to maximize fitness, it yields predictions on a variety of phenomena, including optimal diets, patch choice, and how much time to spend foraging in a patch, as well as movement and visiting rates (e.g., Pyke 1984).

**The metabolic theory of ecology.** The metabolic theory of ecology (MTE) is focused on understanding how the interplay among physiological, ecological, and evolutionary processes both affect and are affected by individual metabolic rate (Brown et al. 2004, West and Brown 2005, Sibly et al. 2012). An underlying premise of the theory is that metabolic rate is fundamental to ecology, because it is through metabolism that organisms interact with their environments.

Over the last 10 years, the **MTE** has yielded two general classes of models.

**The first predicts how two variables**—body size and temperature— affect the metabolic rates of organisms (Spatz 1991, West et al. 1997, Gillooly et al. 2001). This focus on size and temperature is based on early work demonstrating that these variables are each primary determinants of metabolic rate across the diversity of life (Arrhenius 1889, Kleiber 1961, Robinson et al. 1983).

**The second class of models explores** the consequences of metabolic rate at different levels of biological organization, from genomes to ecosystems. Empirical data are generally consistent with predictions of the MTE that size and temperature constrain diverse rate processes, including DNA evolution (Gillooly et al. 2005), population growth (Savage et al. 2004), and ecosystem carbon flux (Enquist et al. 2003, Allen AP et al. 2005, López-Urrutia et al. 2006), through their effects on metabolic rate. Since the MTE yields predictions for these diverse phenomena, given only two parameters—body size and temperature—it represents an efficient theory in ecology. The MTE provides a common frame of reference to make comparisons among organisms that, notwithstanding their different evolutionary histories and ecological settings, obey the same first principles linked to metabolism, size, and temperature. This is exemplified in the application of the MTE to understanding variation in ontogenetic growth rates (figure 2a; West et al. 2001).

### **Some examples of inefficient theories**

For the sake of clarity, it was required to highlight some theories that are not efficient due to having of limited value, but they do not fit some of the characteristics used to define efficient theories.

**R\* or resource-ratio theory.** The body of work represented by R\* or the resource-ratio theory, which has stimulated an enormous amount of research, was first proposed by MacArthur and Levins (1964), then expanded by Tilman (1982) to yield predictions on competition among consumer species for limiting resources. Under competition for a single homogeneously distributed limiting nutrient, R\* theory predicts the winner to be the species that maintains a positive population growth rate at the lowest concentration of the limiting nutrient. It also predicts coexistence of two species when the growth rate of each species is limited by a different nutrient. When resources are heterogeneously distributed, the number of species can be larger than the number of limiting resources, R\* theory is a conceptual advance over previous phenomenological-competition theories, such as the **Lotka–Volterra predator–prey model**, because it predicts the outcome of competition experiments before they are performed. However, it has proven difficult to test, because it has a large number of free parameters (a minimum of three parameters per species–resource combination, in addition to death rates and resource supply rates), which must all be measured to yield predictions. Although the theory is based on the first principles relating population growth to resource supply and consumption, it is not efficient because of its large number of free parameters, which restricts its scope of application

and the possibility of field testing. Nonetheless, it has proven to have heuristic value, which has given rise to several extensions (Leibold 1995, Daufresne and Hedin 2005).

**r/K-Selection theory** : A population ecology concept is r/K selection theory, one of the first predictive models in ecology used to explain life-history evolution. The premise behind the **r/K** selection model is that natural selection pressures change according to population density. For example, when an island is first colonized, density of individuals is low. The initial increase in population size is not limited by competition, leaving an abundance of available resources for rapid population growth. These early phases of population growth experience **density-independent** forces of natural selection, which is called *r*-selection. As the population becomes more crowded, it approaches the island's carrying capacity, thus forcing individuals to compete more heavily for fewer available resources. Under crowded conditions, the population experiences density-dependent forces of natural selection, called *K*-selection. In the **r/K-selection** model, the first variable **r** is the intrinsic rate of natural increase in population size and the second variable **K** is the carrying capacity of a population. Different species evolve different life-history strategies spanning a continuum between these two selective forces. An *r*-selected species is one that has high birth rates, low levels of parental investment, and high rates of mortality before individuals reach maturity. Evolution favors high rates of fecundity in *r*-selected species. Many kinds of insects and invasive species exhibit **r-selected** characteristics. In contrast, a **K-selected** species has low rates of fecundity, high levels of parental investment in the young, and low rates of mortality as individuals mature. Humans and elephants are examples of species exhibiting *K*-selected characteristics, including longevity and efficiency in the conversion of more resources into fewer offspring.

### **Co-evolution of similar interference ability - stabilizing**

**Aarssen** (1983) suggested that, in a mixture of two species, stronger selection pressure on the one with lower interference ability would cause it to become the stronger in interference of the two. Superiority in interference would therefore alternate between the two species' populations, an increase-when-rare situation.

### **Cyclic succession - stabilizing**

The increase-when-rare mechanism here is similar to that of circular interference networks , but the cycle is between vegetation phases, not individual species. Moreover, it can operate with only two phases. Patches are involved, but their environmental differences are autogenic, not allo- genic.. ]

### **Equal chance (neutrality) - equalizing**

It is a long-standing idea that there is an element of chance in which species occurs at a particular spot (Lippmaa 1939; Sale 1977). Chance will make a much larger contribution to species composition when the interference abilities of the species and of individual plants are close to equal (Hubbell 2001; Chesson and Rees 2007). Although Connell (1978) emphasise functionally different, so the equal chance mechanism can never be the sole mechanism of co-existence (Chave 2004). Equal chance is simply a statement that whereas between species with different interference ability one will exclude the other, that process will occur more slowly when the difference is less. The equality in interference ability could arise from co-evolu- tion (see above), but will more commonly be caused by ecological sorting, i.e. the screening out of species with low interference ability. Equal chance is a component ( but only one) of Hubbell's "**Unified Neutral Theory**", and almost all tests of the latter have been weak: failure to find departure from null-model predictions (Lieberman & Lieberman 2007).

### **Initial patch composition - stabilizing**

Levin (1974) proposed a model in which two species occupy small, transient patches. Some patches will by chance have more individuals of one species than the other. If between-species interference is greater than within -species interference, the species in the majority will suppress the other in that patch. Although the model involves spatial differences, the patches are identical in environment so this is not beta-niche differentiation. Evidence required: (a) the existence of **the small-scale meta-community** structure described above; (b) that within-**species interference** is less than between-species

## **EVOLUTIONARY ANALYSIS**

Much previous sociological theory equated evolution with progress or advance- ment. These theories commonly outlined stages of evolution in the develop- ment of societies or

organizations; these evolutionary sequences were typically unilineal and deterministically applied (Granovetter 1979 for a discussion and critique). **Recent ecological theory**, on the other hand, emphasizes the multilineal and probabilistic nature of evolution. Thinking has shifted so much in this direction that, as with **bioecology**, **evolution** is no longer equated with progress, but simply with change over time. In modern organizational ecology, much rethinking is only implicitly evident in the mathematical models used to study change: The time paths predicted by these models can be extremely complex and often contain a large random component. The developmental approach to evolution proponents assume that organizations change structurally over time and that the form of change is shaped by structural pressures and constraints.

**Developmental theory** uses an embryological metaphor (Cafferata 1982) and encompasses much of mainstream organizational theory [Scott (1975)]. This research often is not explicitly ecological, but many of its concepts have been heavily influenced by early ecological theory. For example, organizational conceptualizations of isomorphism and the environment originated in the ecological research of Park (1923, 1929) and Hawley (1950, 1968). The clearest explicitly ecological statement of the developmental approach to organizations can be seen in Kasarda & Bidwell (1984). Briefly stated, this approach casts theory at the organizational level of analysis, using a focal organization perspective. The organization is seen in its environmental context, depending on external resources for sustenance. Environmental conditions constrain the organization and shape organizational structure; however, internal constraints such as size and technology also affect its structure. Theorists differ in the emphasis they place on internal versus external determinants of structure. **Developmental theorists** assume that organizations are highly adaptive: structural changes occur in response to internal and external stimuli. The ecological perspective, however, has always emphasized the noncognitive aspects of these changes (Duncan and Schnore 1959; Hawley 1968). **Ecological theories** of adaptation also tend to be deterministic, to be based on an assumption of temporal equilibrium, and to have an emphasis on symbiosis (Hawley 1968, 1978). Change is also assumed to be irreversible (Cafferata 1982). Recent research using this approach examines organizational life cycles (Kimberly & Miles 1980) and organizational responses to industrial evolution (Miles 1982).

### **The Selection Approach to Evolution**

Despite early attempts by Park (1923, 1929) and more recent efforts by Aldrich (1971) and Kaufman (1975), the selection approach did not blossom until Hannan & Freeman's (1977) paper on the population ecology of organizations. This article directly challenged many of the central tenets of the developmental approach. Hannan and Freeman asserted that organizations are not primarily adaptive, but largely inertial. They argued that the dominant mechanism of social change is natural selection, governed by competition and environmental constraints. They also advocated a shift from the organizational to the population level of analysis and proposed dynamic models of organizational change that are probabilistic and do not assume a state of temporal equilibrium.

### **The Macroevolutionary Approach**

The least explicitly organizational stream of ecological **research is what I call the macroevolutionary approach**. The theoretical logic of this approach is similar to the developmental approach's, although a higher level of analysis is assumed. Whereas developmental theorists focus on change over time in individual organizations, macroevolutionists examine communities of organizations. Macroevolutionary research has developed along two separate lines. **The first** involves analysis of whole societies and is typified by the work of Sahlins and Service (1960), Lenski and Lenski (1974), and Harris (1977, 1979). Researchers using this approach attempt to identify the structural characteristics of societies and to analyze societal changes over long historical periods (Duncan 1964). Historically, empirical work in this tradition has included only global indicators and compared several societies at most. In recent research on the world system, however, many countries are examined simultaneously and multivariate analysis is employed (Wallerstein 1974, Bergeson 1980). **The second line** of macroevolutionary research lies within urban sociology. Emanating from the early Chicago school of Burgess (1925), Park (1926), and McKenzie (1924, 1926), adherents of this tradition examine changes in cities over time and, more recently, in whole systems of cities over time (e.g. Berry and Kasarda 1977, Pred 1966). Although it is truly sociological in character, this research is being increasingly dominated by geographers (but see B. Duncan and Lieberman 1971).

Macroevolutionary research uses much of the logic inherent in the developmental approach. For example, the analyses of organizations by Greiner (1972), of societies by Lenski & Lenski (1974), and of cities by Hawley (1971) all propose deterministic evolutionary sequences for the

transformation of social units over time. The difference in the level of analysis used in the two approaches has profound implications, however. Most importantly, the macroevolutionary approach encompasses organizational selection, while the developmental approach does not. By focusing on large-scale changes in communities of organizations, macroevolutionary research in essence describes the rise and fall of organizational forms (sometimes referred to as succession).

### **Evolutionary Stable Strategy (ESS)**

**Evolutionary Stable Strategy (ESS)** advocates that inheritable traits within a specified population oppose the intrusion of any such traits or mutant variety of other populations in order to retain the existing genotypes avoiding the replacement of the existing variety. This ESS being an important approach in understanding and explaining the behavioral manifestation of animals, especially valuable in the discretely phenotypes which interact with one another (Smith and Price, 1973; Parker, 1984). John Maynard Smith (1982) explains ESS as such a strategy that that resist the invasion of mutant strategy by the combined strength of all the individuals of a population .Dispersal is said to be an evolutionary stable strategy as a population in the process of dispersal dispersers facing no selective pressure can achieve that tendency (ESS) ( Maynard Smith, 1972) .

### **Game theory :**

This theory depicts the ecological relationships within a community ( assemblages of species or of traits under the command of those organisms) can be regarded as a contest i.e. a game in which each biotic component solicits to have some advantages. Numerical values are used to evaluate the losses and gains mathematically on devising computer modeling. The application of game theory has produced many insights into ecological relationships and the significance of particular aspects of animal behavior. The game theory alongside explaining the behavioral evolution by considering both the costs and benefits of several behavioral decisions of

individuals who are endeavoring unconsciously to maximize their reproductive success. The proponents of this theory focus the cases when competing individuals displaying fitness consequences of a given behavioral option, depend on the actions of the other competitors. In such context, decision making is treated as game in order to understand the choices made by people as they compete with one another for their benefit in respect of resources, One of the noted evolutionary biologists. W.D. Hamilton, was pioneer in thinking about evolution as a game between competing phenotypes where he argued that best suited ecological conditions enable a individuals lived alone by adopting its own behavioral strategy The end result , according to Hamilton , could be a selfish herd in which all individuals were trying to hide behind others to reduce the probability of being selected by a predator.

### **The Macro-evolutionary Approach**

The theoretical logic of macro-evolutionary approach seems to differ from the developmental approach of developmental theorists who tend to focus on change over time in individual organizations, whereas macro-evolutionists examine communities of organizations. Macro-evolutionary research has resulted dichotomous interpretations of the ecological findings :

**The first involves** analysis of whole societies where the researchers using this approach with an objective to identify the structural characteristics of societies and to analyze societal changes over long historical periods (Duncan 1964).

**The second line** of macroevolutionary research revolves within urban sociology examining the changes in cities over time and, more recently, in whole systems of cities over time utilizing much of the logic inherent in the developmental approach to derive understanding from the deterministic evolutionary sequences for the transformation of social units over time.

**Evolutionary ecology is** an important focus for problems of adaptation and studies of natural selection in population (Krebs, 1994 )

**ESS** , an approach for understanding adaptation, particularly useful in the discretely phenotypes and when the phenotypes interact with one another, is that of determining the evolutionary stable strategy (Smith and price, 1973; Parker, 1984) .The ESS is that phenotype or combination of phenotypes that when constituting a population, makes it impossible for individuals wiyh



alternative phenotypes to invade the population. As John Maynard Smith (1982) puts it , as ESS is " **strategy such that , if all the members of a population adopt, no mutant strategy can invade. "**

**Evolutionary Stable Strategy (ESS)** states that traits or combination of traits that operate in a given population resist the intrusion of any such traits or mutant variety so that the replacement of the existing variety may be avoided. This ESS play important roles in explaining the behavioral manifestation of animals.

Dispersal is said to be an evolutionary stable strategy (ESS) ( Maynard Smith, 1972) . A population of non-dispersers will evolve towards the ubiquitous possession of a dispersive tendency; but a population of dispersers will be under no selective pressure to lose that tendency.(Begon et al 2005 )