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## The general thesis

The argument developed in this book is that much of the evolved nature of a species or higher taxon has a direct causative influence on the central issues concerning the ecology of that taxon: distribution, abundance, and population dynamics. Therefore, the macroevolutionary basis of a taxon is essential for understanding the fundamentals of ecology. This approach has not been advocated or subscribed to in the literature, neither in classical ecological texts such as Allee *et al.* (1949), Andrewartha and Birch (1954), and Odum (1959), nor in current volumes (e.g. Colinvaux 1993; Begon *et al.* 1996; Ricklefs 1997; Stiling 1998; Ricklefs and Miller 2000). More specialized approaches to population ecology emphasize direct environmental conditions rather than the overarching involvement of macroevolution (e.g., Royama 1992; Brown 1995; Den Boer and Reddingius 1996; Rhodes *et al.* 1996; Hanski and Gilpin 1997).

The study of the distribution, abundance, and population dynamics of species has been a central focus for ecologists for at least a century, as emphasized by Andrewartha and Birch (1954). "Ecology is the scientific study of the interactions that determine the distribution and abundance of organisms" (Krebs 1994, p. 3). Driven by pragmatism, the need to understand populations was prompted by burgeoning human populations (e.g. Malthus 1798; Verhulst 1838; Pearl and Reed 1920), plagues of agricultural pests (e.g. Waloff 1946), defoliating forest insects (e.g. Bodenheimer 1930; Schwerdtfeger 1941), human diseases, and the vectors of etiological agents (e.g. Smith and Kilbourne 1893; Zinsser 1935; Manson-Bahr 1963). Therefore, a paradigm shift in the conceptual basis of such central issues in ecology should be of consequence for the majority of ecologists.

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## MACROEVOLUTION AND MACROECOLOGY

The terms macroevolution and macroecology are established in the literature. Macroevolution denotes evolution above the species level: the origin of new species, genera, families, etc., and the resulting phylogenetic relationships among taxa. The benefit of a macroevolutionary approach to ecology is that phylogenetic relationships provide the strongest and most extensive patterns to be found in nature. A comparative macroevolutionary approach provides a powerful and encompassing method for discovering and understanding ecological patterns. Macroecology was defined by Brown (1995, p. 10) as “a way of studying relationships between organisms and their environment that involves characterizing and explaining statistical patterns of abundance, distribution, and diversity.” In their original discussion of macroecology, Brown and Maurer (1989, p. 1145) emphasized its involvement with the “analyses of statistical distributions of body mass, population density, and size and shape of geographic range.” Lawton (1999, 2000) embraced the term macroecology and the statistical nature of its methodology. However, as Root (1996, p. 1311) noted in his insightful review of Brown’s book, “only a few kinds of data, on traits that are relatively easy and straightforward to measure (e.g. body mass, length of appendages, geographic range), are available in sufficient quantity for analysis.” Such constraints limit the development of this field.

In this book the term macroecology is extended to its logical limit, involving the study of broad patterns in ecology. This definition incorporates the topics covered by Brown and Maurer and becomes equivalent in scope to the term macroevolution.

## THEORY AND HYPOTHESIS

Setting distribution, abundance, and population dynamics in a macroevolutionary and macroecological framework places these central themes in ecology on a far larger scale than in the past, affording a strongly comparative approach to the understanding of broad patterns in nature. I define scientific theory simply as the mechanistic explanation of broad patterns in nature. The patterns must be empirical and the explanations must be factual. This is the Darwinian concept of theory and the Darwinian approach to the development of theory. Only with this Darwinian view will scientific theory in ecology achieve its potential of accounting for broad patterns in nature. Thus my use of the term theory is in the narrow sense of truly mechanistic explanation of broad patterns in nature, as in the modern theory of evolution. A

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clear distinction is made between the term hypothesis, being an idea in need of more testing, and a theory, which is factually based and well tested, with the weight of evidence consistent with the main thesis. Darwin provided a profoundly insightful hypothesis on evolutionary mechanisms, but with factually flawed mechanistic explanations for the origins of variation in populations and the hereditary process. Nevertheless, the empirical observations that variation in populations persisted and that traits were passed down through generations were sufficient to render his hypothesis the basis for the modern theory of evolution. This book starts with an hypothesis, presents information and methodologies that test the hypothesis, and ends with an argument supporting acceptance of the hypothesis as theory.

Theory based on empirical patterns and explanations contrasts with much of so-called theoretical ecology which is largely devoted to hypothetical investigation. "As with all areas of evolutionary biology, theoretical development advances more quickly than does empirical evidence," wrote Johnson and Boerlijst (2002, p. 86). My view is that empirical pattern detection is primary. This then motivates the search for mechanisms, and if the pattern is broad its combination with a mechanistic explanation results in theory. Therefore, empirical studies direct the development of theory – a fully Darwinian view.

One of the major problems with ecology today is the existence of too much data and not enough theory, too many hypotheses and not enough testing, too many models and not enough verification. "Ecology is awash with all manner of untested (and often untestable) models, most claiming to be heuristic, many simple elaborations of earlier untested models. Entire journals are devoted to such work, and are as remote from biological reality as are faith-healers" (Simberloff 1980, p. 52). Models and hypothetical theory can be readily defended (e.g. Caswell 1988), but development of factually and empirically based broad patterns and their mechanistic understanding must surely advance the science of ecology more rapidly than any other component in this scientific endeavor.

Factual theory in ecology must cope with the tremendous diversity of organisms and phylogenetic pathways, recognizing that several to many outcomes are possible because of evolutionary and ecological processes. Theory must be pluralistic. Beginning with taxon A under ecological conditions B, the outcome will be C. With taxon A in different conditions D, the result may be E (cf. MacArthur 1972a). Outcomes are obviously conditional on the inputs and prevailing conditions, so that we should anticipate different results when different

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organisms evolve in the same environment or if the same organisms evolve in different environments. Theory must recognize the different phylogenies and conditions in which member species have evolved, and embrace pluralism as much as is needed, dictated by the relative conformity or diversification of the taxa under study. Ending their critique of the adaptationist or “Panglossian paradigm,” Gould and Lewontin (1979, p. 597) endorsed the pluralistic approach:

We welcome the richness that a pluralistic approach, so akin to Darwin’s spirit, can provide. Under the adaptationist programme, the great historic themes of developmental morphology and *Bauplan* were largely abandoned; for if selection can break any correlation and optimize parts separately, then an organism’s integration counts for little. Too often, the adaptationist programme gave us an evolutionary biology of parts and genes, but not of organisms. It assumed that all transitions could occur step by step and understated the importance of integrated developmental blocks and pervasive constraints of history and architecture. A pluralistic view could put organisms, with all their recalcitrant, yet intelligible, complexity, back into evolutionary theory.

This, in my view, is precisely what is needed in ecology. A pluralistic view, recognizing patterns resulting from different phylogenetic origins and *Baupläne*, and the macroevolutionary divergence of lineages, will bring ecology into a central place in evolutionary biology. Unless we embrace a macroevolutionary view of ecology we will remain collectors of facts, piles of facts, without theory to guide progress. We have piles of studies on plant and herbivore interactions, chemical ecology, and multitrophic-level interactions, but extraordinarily little pattern detection and certainly no factually based theory that is broadly supported and widely subscribed to: “a pile of sundry facts – some of them interesting or curious but making no meaningful picture as a whole” (Dobzhansky 1973, p. 129).

The field of ecological morphology is already well established. “Ecological morphology is broadly concerned with connections between how organisms are constructed and the ecological and evolutionary consequences of that design” (Reilly and Wainwright 1994, p. 339). The explicit assumption is that morphology has direct effects on ecology, a view heretofore absent in the sciences relating to population dynamics.

## QUESTIONS

If we are to address broad patterns in nature and the underlying mechanisms driving pattern, there must be a set of broad questions to focus

upon. These are far broader than generally conceived, especially relating to population dynamics. For example, why are some insect taxa replete with serious pest species, such as the short-horned grasshoppers, while others are full of innocuous and inconspicuous species, such as the tree hoppers? The acridid grasshoppers include the worst pests on earth in the form of plague locusts, but tree hoppers or membracids hardly enter into books on harmful insects. Even more closely related taxa can exemplify very different patterns of distribution, abundance, and population dynamics. We may well ask, why does one group so frequently show epidemic or outbreak dynamics, such as the pine sawflies, while its sister taxon contains very few outbreak species, as in the common sawflies? The pine sawfly family, *Diprionidae*, includes in North America almost 85 percent of species that are serious forest pests (Arnett 1993), but the family of common sawflies, *Tenthredinidae*, contains only about 3 percent that are regarded as pests (Price and Carr 2000).

Following such questions on broad patterns in nature there are the obvious additional questions on mechanisms. Why are outbreak, eruptive, or pest species so different in their population ecology from the many species that are patchily distributed, of low abundance over a landscape, and with relatively stable population dynamics? Why are some phylogenetically divergent taxa so similar in their population ecology? Specific taxa will be used to address and resolve these questions.

#### THE CENTRAL HYPOTHESIS

We have called our thesis the **Phylogenetic Constraints Hypothesis** (Price 1994b; Price *et al.* 1995a, 1998a; Price and Carr 2000). Its conceptual framework is developed best in Price and Carr (2000). The empirical observations and experiments, and the discovery of natural patterns, which initially prompted development of the hypothesis, are described in Chapters 3–5. The hypothesis argues that macroevolutionary patterns provide the mechanistic foundation for understanding broad ecological patterns in nature involving the distribution, abundance, and population dynamics of species and higher taxa. A **phylogenetic constraint** is a critical plesiomorphic character, or set of characters, common to a major taxon, that limits the major adaptive developments in a lineage and thus the ecological options for the taxon. However, many minor adaptations become coordinated to maximize the ecological potential of a species within the confines of the phylogenetic constraint. This

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set of adaptations constitutes the **adaptive syndrome** of the group. The adaptive syndrome has inevitable ecological consequences, named **emergent properties**, involving distribution, abundance, and population dynamics.

This hypothesis differs fundamentally from existing approaches to population ecology. Most current hypotheses are ecological and idiosyncratic, based on the study of single species, exemplifying the **idiographic program**, as expanded upon in the next chapter. The Phylogenetic Constraints Hypothesis is evolutionary, strongly comparative, and synthetic in its treatment of taxonomic groups higher than the species level, emphasizing basic mechanistic processes and broad patterns in nature: a truly **nomothetic approach** to population ecology: the **Macroevolutionary Nomothetic Paradigm**.

The terms we use in the Phylogenetic Constraints Hypothesis are established in the literature, although the mechanistic pathway of cause and effect is new, starting with our treatment in Price *et al.* (1990). McKittrick (1993, p. 309) defined a phylogenetic constraint as “any result or component in the phylogenetic history of a lineage that prevents an anticipated course of evolution in that lineage.” Thus, a constraint limits the adaptive radiation of a lineage in a certain manner, such that the full potential radiation is not achieved. Such constraints are likely to have **phylogenetic effects** in the sense of Derrickson and Ricklefs (1988), meaning that closely related organisms are likely to be similar in their evolved characters of morphology, physiology, behavior, life history, and ecology.

The term adaptive syndrome was coined by Root and Chaplin (1976). “As organisms perfect a mode of life, their evolution is channeled so that a variety of adaptations are brought into harmony” (p. 139). This integrated set of adaptations was defined by Eckhardt (1979, p. 13) as “the coordinated set of characteristics associated with an adaptation or adaptations of overriding importance, e.g. the manner of resource utilization, predator defense, herbivore defense, etc.” We use the term in this sense while arguing that the adaptive syndrome we assert to be central is that in relation to the phylogenetic constraint. That is, the syndrome is a set of adaptations that mitigate the effects of the constraint and may even turn it into some kind of advantage. As Ligon (1993, p. 3) said, “yesterday’s adaptation may be today’s constraint,” but the reverse is also true.

An emergent property is one that arises as a natural or logical consequence or outcome. Brown (1995) used the term in this way. The term is often used, also, as a property that is unexpected and not predicted

based solely on the knowledge of components, as in the combination of hydrogen and oxygen to make water (cf. Mayr 1982). For ecologists, Salt (1979, p. 145) recommended the operational definition: "An emergent property of an ecological unit is one which is wholly unpredictable from observation of the components of that unit." Whichever definition is preferred, our use complies. The argument we make that major patterns in distribution, abundance, and population dynamics are driven by mechanisms dictated by the evolved phylogenetic baggage of lineages is clearly unexpected based on the relevant literature discussed in Chapter 2. The argument can be developed only after detailed study of one species and its relatives, and must be based on a clear understanding of the evolutionary biology of the group. These points are covered at length in Chapters 3 and 4. And, just as we can now confidently predict that oxygen mixed with hydrogen will yield water, we can logically predict much of the ecology of a taxon based on its phylogenetic constraints and adaptive syndrome. In fact, our research program is akin to that of Sih *et al.* (1998) on emergent impacts of multiple predator effects (MPEs) on prey. They note that "Ultimately, our goal is not just to document the existence of emergent MPEs but to identify characteristics of predators, prey or the environment that tend to make one type of emergent effect . . . more likely than another" (Sih *et al.* 1998, p. 354). This is precisely the research focus of our program over the past decade, but relating to the emergent properties of population dynamics (e.g. Price *et al.* 1990, 1995a, 1998a; Price 1994b).

Ideally we should adopt a formal phylogenetic analysis of a clade mapping evolved traits on the phylogenetic hypothesis and the correlated emergent properties concerning distribution, abundance, and population dynamics. Such an analysis is not yet possible for any group because especially the population dynamics of many species in a taxon is not adequately documented. However, for the first time we do map population-level traits on a phylogeny, showing the causal linkage from a phylogenetic constraint to the adaptive syndrome to the emergent properties. Although the criteria used for the emergent properties are subjective more than quantitative, this first example provides a methodology for a rigorous test of the Phylogenetic Constraints Hypothesis (see Chapter 5).

Although the flow of effects from phylogenetic constraints to adaptive syndrome and its emergent properties forms the central theme of our thesis, at all steps resources intersect with evolutionary developments. Thus, the nature of resources utilized by insect herbivores must be understood in detail. Indeed, the display of resources may even

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override strong phylogenetic constraints, resulting in divergent adaptive syndromes and emergent properties, as explained in Chapter 8. However, I consider such strong effects to be unusual and more subtle influences to be more general among herbivorous insects. For example, differences in resources for the herbivorous Hymenoptera, sawflies and woodwasps, result in dramatic variation in ovipositor morphology but the *Bauplan*, including the lepismatid form of ovipositor, remains intact throughout. Among the most important biological features in the Hymenoptera, Gauld and Bolton (1988, p. 8) have the “ovipositional mechanism” first. But the interplay of the hymenopteran ovipositor and resource heterogeneity becomes a central issue in Chapter 3.

The novelty of the arguments developed in the Phylogenetic Constraints Hypothesis can be evaluated only in the light of past and current general views on the factors that influence the population dynamics of species. Therefore, I provide a brief historical overview of the field in Chapter 2. Then I progress to coverage of the focal species on which this hypothesis was developed, in Chapters 3 and 4, and to related species in Chapter 5. The importance of comparative studies across a taxon must be emphasized if we are to search for general patterns, mechanisms, and empirically based theory. The comparative approach is then extended in Chapter 6 to other taxa with similar constraints but more divergent phylogeny. Very different species with different dynamics are discussed in Chapter 7, sister taxa with divergent emergent properties are discussed in Chapter 8, and an attempt is made to advance the hypothesis into the world of vertebrates and plants in Chapter 9. Finally, Chapter 10 is devoted to a synthesis on the distribution, abundance, and dynamics of organisms.



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## Historical views on distribution, abundance, and population dynamics

A brief historical perspective on demography, distribution, abundance, and population dynamics is essential for an appreciation of the paradigmatic shift advocated in this book. Such a view is provided in various sources by experts, which can be consulted for details, and from which I have constructed some of the scenario presented here. In their *Principles of animal ecology*, W. C. Allee, Alfred E. Emerson, Orlando Park, Thomas Park, and Karl P. Schmidt (1949) devoted Section I to the history of ecology up to 1942. Their authoritative view is valuable because they had experienced first hand much of the development of ecology during the twentieth century. Two books published in 1954 also became classics in ecology: David Lack's *The natural regulation of animal numbers* and *The distribution and abundance of animals* by H. G. Andrewartha and L. C. Birch, providing these authors' perspectives on the state of the field in the mid 1950s. LaMont Cole (1957) wrote an excellent review on the history of demography, and Tamarin (1978), in the Benchmark Papers in Ecology series, provided a balanced treatment on *Population regulation* with readings covering major points of view through the controversial 1960s and into the early 1970s. From the early 1960s I have worked in this field of ecology, so I will provide a more personal view of developments since then. First, I will concentrate on how ideas developed into the 1950s based on field studies and other empirical methods. Then I will discuss demography and the emergence of life table analysis, followed by trends up to the present day.

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### EARLY FIELD STUDIES

Because my prime concern in population dynamics is the insects, and the study of insects has provided the basis for my macroevolutionary approach, a gratifying detail is the early concentration of population

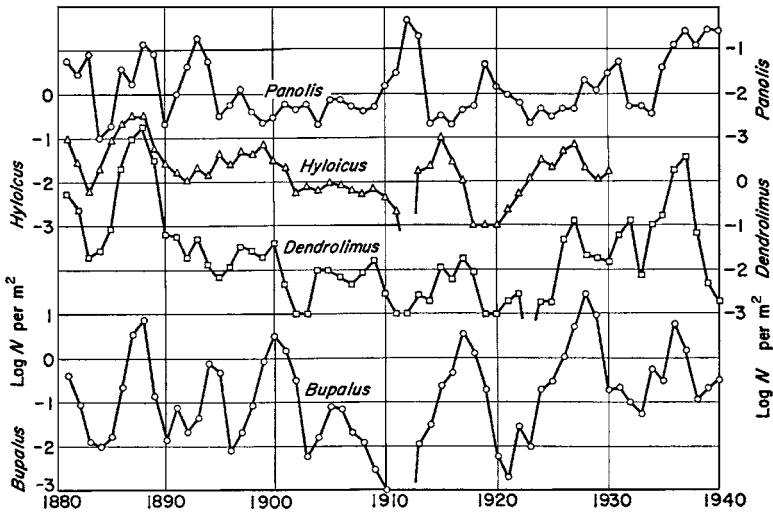


Fig. 2.1. Population densities of four forest insects in Letzlinger Heide, Germany, sampled from 1880 to 1940. The species were the pine beauty moth, *Panolis flammea* (Noctuidae), the pine hawk moth, *Hyloicus pinastri* (Sphingidae), the pine spinner moth, *Dendrolimus pini* (Lasiocampidae), and the bordered white moth, *Bupalus piniarius* (Geometridae). Densities, plotted on a logarithmic scale, are winter census estimates of number of moth pupae per m<sup>2</sup> in the soil for *Panolis*, *Hyloicus*, and *Bupalus*, and the number of hibernating larvae per m<sup>2</sup> of forest floor for *Dendrolimus*. (From Varley, G. C., G. R. Gradwell, and M. P. Hassell (1973) *Insect population ecology*, Fig. 8.2, Blackwell Science, Oxford; based on Varley 1949.)

studies on forest Lepidoptera in Germany. Chronology of outbreaks was recorded for major insect species starting in 1801 in Bavarian areas with a record for 188 years (Klimetzek 1990). As a subset of these surveys, four species of moth were censused for 60 years from 1880 to 1940 (Fig. 2.1), although as in many studies since, a mechanistic understanding of the fluctuations was not achieved (Schwerdtfeger 1935, 1941). Schwerdtfeger rejected any simple explanation such as weather or parasitic wasps and flies, recognizing that many factors may be important and each may affect the four species in different ways and at different times. Varley (1949) attempted a new analysis of the data, but concluded that insufficient data were provided for an informed interpretation. "Let us hope that further work will be concentrated on producing the detailed mortality and fertility data which may eventually help to provide a proper explanation of these fascinating problems"