

The Turbulent Marriage of Ecology and Evolutionary Biology

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ABSTRACT: This paper examines the alliance between ecology and evolutionary biology, which has been a distinct program of biological research for more than a century now. In particular, it focuses on a part of this program that is the most visible theoretically and empirically: the unification of population ecology and population genetics, which has been in progress for more than half a century now. The motivation for this paper is scientific as well as philosophical: the former because of the potential benefits of a synthesis to both disciplines and to biology, and the latter because the interface between ecology evolution appears to be a fertile ground for philosophical work. I begin by highlighting the disparities between ecological and evolutionary viewpoints and review aspects of their history that point at the roots of discord as well as efforts for synthesis. There appear to be three important differences in viewpoints that population genetics and population ecology differ at: the role of processes at different time-scales, demographic considerations (including measures of fitness), and environmental heterogeneity. Based on these, a taxonomy of contemporary theoretical approaches that merge these two disciplines is attempted, with focus on their conceptual approach, themes of research, and empirical advances. This allows an evaluation of the current status of the synthesis; it is clear that the unification of population biology through an evolutionary ecology synthesis has made steady progress, but remains a work in progress. The nature of this unification also calls for a re-evaluation of the reasons for which ecology has been considered a sterile subject by philosophers. The current structure of the synthesis clearly indicates a balanced role for the two disciplines in the conceptual advancement of biology, and philosophers should perhaps pay more attention to the progress of this synthesis. This will also perhaps be a refreshing diversion from the rather bedraggled issue of the existence of laws in ecology and in biology.

“‘If there's no meaning in it,’ said the King, ‘that saves a world of trouble, you know, as we needn’t try to find any...’” – Alice in Wonderland

1. INTRODUCTION

Few would hesitate in identifying ecology and evolutionary biology as areas of research with disparate goals. We generally imbibe their theory and practice separately; one need only flip through an introductory text in biology to see how well-established this dichotomy is. However, the motivation for this paper is not pedagogic. A majority of the practitioners of either discipline conduct research without an iota of perspective from the other and one of my objectives is to examine whether this approach, somewhat akin to King’s view in *hinders each discipline’s progress*ⁱ, the sources for discord in what is oft broached as a much needed collaboration, and the current status of such enterprise. This is an appropriate juncture to make this evaluation, as the last decade or so has seen a surge of theoretical and empirical work aimed at combining ecological and evolutionary perspectives.

This first, largely scientific line of investigation is tied to another, more philosophical motivation for this paper. Ecology has been noticeably underrepresented in accounts of the philosophy of biology (e.g., Hull 1974; Sober 1993; Grene and Depew 2004). This reflects a disinterest, the reasons for which are worth exploring. This paper will argue that both cultural and conceptual differences between these disciplines have hindered their synthesis, and that this discord, and the nature of the current synthesis themselves are fertile grounds for philosophical analyses. Moreover, by highlighting the interdependence of ecological and evolutionary theory, and the importance of a synthesis to the overall progress of biology, this paper will also oppose the widespread view that ecology appears dull to philosophers because in its classical mold it is theoretically and causally redundant within biology (e.g., Haila and Taylor 2001).

Ecology today comprises of a heterogeneous array of disciplines, transcending levels of complexity from individuals and populations at one end to ecosystems at the other. An attempt to examine the role of evolutionary biology at each of these and vice versa is beyond the scope of this paper. I will therefore focus mainly on two fields that form the traditional foundation of ecology and evolutionary biology, and who have a long history of exchange and attempted union: population biology and population genetics. Nevertheless, instances where such a union has obvious implications for higher levels of complexity will be dwelt upon. In the following sections, the following issues are addressed:

- (i) Goals of contemporary ecology and evolutionary biology.
- (ii) A brief review of historical relationship with focus on perceptible roots of discord as well as attempts for collaboration between themⁱⁱ.
- (iii) Current sources of discord between the two disciplines.
- (iv) Based upon the approach taken towards resolving these differences, a classification of current research themes in evolutionary ecology.
- (v) The current status of this synthesis in light of recent theoretical and empirical advances.
- (vi) And finally, a discussion of philosophical implications in light of the preceding results.

2. THE ROOTS OF DISHARMONY

2.1 Contemporary ecology vis-à-vis evolutionary biology

Ecology today covers a wide range of topics ranging from the level of the individual, to ecosystems. This naturally implies a varied set of objectives, but a common underlying theme can still be identified as being along the lines of what the inventor of the term Haeckel (see below) originally defined it: the relationship between organisms and their environmentⁱⁱⁱ. These two elements also comprise distinct ways in which things “ecological” are taken to mean: to some, ecology is synonymous with the characteristics of individuals, populations, communities or ecosystems of organisms, while to others, ecology is the environment that affects the organisms. This environment of course, can be biotic as well as abiotic.

Disciplines in contemporary ecology are largely devoted to analyses of patterns observed in nature, their origins, and their changes with respect to the environment. Compared to evolutionary biology, ecology tends to dwell more in the present, its practitioners being most concerned with the relationship between organisms and their biotic as well as abiotic environment in “ecological time scales” (temporal scales in the order of one of few generations of the studied organisms). The common approach used to study these aspects is a mechanistic, physical one, with a tacit assumption of purely non-evolutionary response, and without consideration of the genetic variation (Mayr 1997, pp. 210-211). Relative to evolutionary biology, the hope for general principles that govern these relationships have spurred the development of a very detailed analyses of organism-environment interactions.

Evolutionary biology on the other hand, consists of both prospective and retrospective theoretical frameworks that are concerned with the origins of, and changes in living entities over varying time scales. At one end lies the mathematical theory of genetics that forms a basis for microevolutionary (evolution on relatively short temporal scales) research. At the same time, the fecund collaboration of molecular biology and classical evolutionary theory (cf. Huxley 1942) now also contributes to macroevolutionary (evolution over longer, generally geological time scales) research through an increasing collaboration between phylogenetics, systematics, and paleontology. I now present a brief historical background with the objective of exploring the roots of discord as well as collaboration between these two disciplines.

2.2 An early association and subsequent divergence: 1850-1950

The history of evolutionary biology and ecology from 1850 to 1950 provides interesting insights into their early relationship. As with so many other topics in biology, Darwin (1859) is a good place to begin because it was simultaneously the birth of evolutionary biology as we know it today, and the explication of the relationship between the organism and the environment, which prompted Haeckel to coin the term *ökologie* in 1866 (Haeckel 1866)^{iv}. In his words, ecology was “...the investigation of the total relations of the animal both to it's in organic and to its organic environmentin other words, ecology is the study of all those complex interrelationships referred by Darwin as the conditions for of the struggle for existence” (quoted in Stauffer 1957). Naturally, the first step towards achieving this goal was to study the effect of the environment on individuals and populations.

The period from the Haeckel's definition to the beginning of the 19th century was a crucial period for the discipline, although the term “ecology” was not used much. This was when the tradition of detailed botanical and zoological study of morphology, anatomy and physiology of the individual in relation to its adaptive environment was established. This was also the period when Herbert Spencer published his ideas about the emergence of order in nature (Spencer 1864), which strongly influenced the approach of future generations by embedding the notion of stability and the “balance of nature” in the ecological psyche. By the beginning of the 20th century when the units of study in ecology had already been defined at multiple levels beyond the individual, and population as well as community ecology we coming to the fore as distinct disciplines, a strong belief in the equilibrium state of nature of the units of life had already taken hold. This was followed by an adoption of a physical view by many ecologists, wherein living units were transformers of energy enmeshed in larger systems with considerable resilience to perturbation, and where details of the evolutionary process could be glossed in interest of a more systemic approach (The beginnings of “systems ecology”; Kingsland 1985, pp. 34-49)

Apart from the systems approach to ecology, this was also the period when faith in the pre-adaptation of species and the slowness of evolution took firm hold. These beliefs freed the ecologist of evolutionary concerns, and allowed a single minded commitment to the study of the nature of the adaptations in relation to the environment. The roots of the viewpoint that ecology and evolution operate at vastly different time scales are probably to be found in fact that including Darwin's work, early evolutionary ideas were based on the fossil record, and tended to be “gradualist”(Stanley 1989). In Darwin's words, (Darwin 1859, pp. 126-127) “I do believe that natural selection will generally act very slowly, only at long intervals of time, and only on a few of the inhabitants of the same region. I further believe that these slow, intermittent results accord well with what geology tells us of the rate and manner at which the inhabitants of the world have changed.” This view was

reinforced by the fact that examples of natural life tangible to early observers mostly happened to be relatively long-lived vertebrates.

Thus in its development through the first part of the 20th century, the rapidly proliferating branches of ecology had largely diverged from evolutionary biology with only sporadic exchange between the two disciplines. Ecologists during time focused increasingly on the effect of the abiotic environment and biotic interactions on populations to the exclusion of any considerations of genetics or evolution, trying to deal with the onerous task of defining the characteristics and emergent properties of the various levels individuals to ecosystems.

The “The golden age of theoretical ecology” from 1920 to 1940 (Scudo and Ziegler 1978), was marked by the rediscovery of the Verhulst logistic equation by Raymond Pearl in the 1920’s and its extension to interacting populations, as well as experimental evaluation (e.g., Gause 1934; op. cit. Kingsland 1985). The approach of theoretical ecology then was to define state variables representing properties of the population as a whole with a tacit assumption of genetic homogeneity. For example, the coupled differential equations of the classic Lotka-Volterra equations of competition between two species with population sizes N_1, N_2 ,

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1 + \alpha_{12} N_2}{K_1} \right) \\ \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2 + \alpha_{21} N_1}{K_2} \right)\end{aligned}\tag{1}$$

include the following immutable state parameters: r_1, r_2 (intrinsic growth rates of species’ 1&2), K_1, K_2 (carrying capacities), and α_{12}, α_{21} (coefficients of competition). It is clear that many of the pioneers of theoretical population biology during this period were, to various degrees, motivated by Darwin’s theory of natural selection and the then prevalent schools of evolutionary thought^v. This period also coincided with the mathematical fusion of Mendelian genetics and Darwin’s theory by Fisher, Haldane and Wright (the “Modern Synthesis” of evolutionary biology; Huxley 1942).

Both population ecology and population genetics had, and still do, the same mathematical foundations at their core. For example, consider the case of an asexual haploid population with discrete, non-overlapping generations. Let time be measured in generations, such that population size at time t , $N(t)$, is the result of the previous generation’s population size, $N(t-1)$ multiplied by a growth factor which combines survival and reproduction, say w . Thus,

$$N(t) = wN(t-1) = w^2(N(t-2)) = \dots = w^t(N(0))\tag{2}$$

yielding the classical model of population growth in discrete time. It is straightforward to extend equation (2) in population genetics terms. The growth factor w is the absolute fitness of the population, and can be written as $w = 1 + s$, such that the population increases if $s > 0$ and decreases if $s < 0$. The change in population size then is,

$$\Delta N(t) = N(t+1) - N(t) = (1+s)N(t) - N(t) = sN(t)\tag{3}$$

Now, suppose the population contains k kinds of genotypes (alleles), each with its own growth rate (fitness), $w_i = 1, 2, \dots, k$. Let $n_i(t)$ denote the population size of genotype i at time (=generation) t . Then, total population size at time t , $N(t) = \sum_i n_i(t)$, and the mean fitness of the population is

$$\bar{W}(t) = \sum_{i=1}^k W_i \frac{n_i(t)}{N(t)}\tag{4}$$

\bar{W} will change over generations with changes in n_i . A continuous time extension of the population growth model shows the relationship between the population biologist's Malthusian parameter r (also known as the intrinsic growth rate) and fitness W . Consider the population growth in continuous time $\lim_{dt \rightarrow 0} \frac{dN}{dt} = rN$,

which has the solution,

$$N(t) = N(0)e^{rt} \quad (5)$$

This is the familiar equation of exponential population growth. Then by comparing eqns. (5) and (2), $w = e^r$ or $r = \ln(w)$. If w is close to 1 (population size is not changing), i.e., $s < 1$, $\ln(w) = \ln(1 + s) \approx s$, or $r \approx s$, thus allowing the Malthusian parameter to be used as a measure of fitness. This illustrates the interchangeability of the core concepts in population genetics and ecology, under some assumptions.

During this coincident period of the development of population genetics and population biology however, little effort was made to combine the theories, although there were voices such as Elton (1927) and Gause (1934) that espoused the importance of exchange between the two disciplines. In part, this was because the extensions of models such as eqns. (1) by themselves posed mathematical challenges without introducing the added complexity of genetics. Another reason is that these early voices of evolutionary ecology were drowned in the clamor created by the rapid proliferation of ecological subdisciplines (Kingsland 1985). For example, Gause, who was clearly motivated by Darwin's theory (see introductory remarks in Gause 1934), expressed the desire to eventually combine the population ecology of Volterra with the mathematical genetics of Haldane and others, but apparently never attempted this (Kingsland 1985, p. 160). A rare example of such work appears to be that of V. A. Kostin, whose efforts however passed largely unnoticed, and were cut short by the Second World War (Kingsland 1985, p. 144)^{vi}.

On the other hand, the direction taken by evolutionary theorists during the early 20th century also resulted in disassociation from many aspects of ecology. The foundations of Mendelian population genetics were built by a bare-bones approach of achieving mathematical tractability by judicious approximation and selective omission of ecological reality. For instance, as shown above, approximation of the Malthusian parameter r by the selection coefficient s involved assumption of a fixed population size. The Hardy-Weinberg "theorem" served as a useful model by allowing an estimation of expected allele frequencies in diploid populations under assumption of panmictic, random mating, infinitely sized populations that experience no selection, mutation, emigration or immigration. A relaxation of different assumptions then allowed a modeling of the various agents of evolution, an approach that is still used in classical population genetics.

For example, a traditional approach to modeling the role of natural selection in a diploid sexual population is to track the changes in allele frequencies for a single locus and two alleles. Consider two alleles 1 & 2, with frequencies p & q , respectively. Assume an infinite population size, which assures that there is no random loss of alleles (no genetic drift), and that the condition of fixed population size derived in eqns. (2-5) is satisfied. Furthermore, assume completely random mating followed by selective mortality, such that zygotes in every generation are in Hardy-Weinberg (HW) proportions of p^2 , $2pq$ and q^2 before selection. Denoting population sizes of the three genotypes as N_{11} , N_{12} , N_{22} , and assigning fitnesses w_{11} , w_{12} and w_{22} (loss of zygotes from mortality followed by reproductive gain) respectively, the number of individuals of each genotype in the next generation are, $N_{11}' = w_{11}N_{11}$, $N_{12}' = w_{12}N_{12}$ and $N_{22}' = w_{22}N_{22}$. Then the frequency of allele 1 in the next generation is,

$$p' = \frac{N_{11}' + \frac{1}{2}N_{12}'}{N_{11}' + N_{12}' + N_{22}'} = \frac{w_{11}N_{11} + w_{12}\frac{1}{2}N_{12}}{w_{11}N_{11} + w_{12}N_{12} + w_{22}N_{22}} = \frac{w_{11}p^2 + w_{12}pq}{w_{11}p^2 + w_{12}2pq + w_{22}q^2} \quad (6)$$

Now, dividing throughout by w_{11} adds the convenience of reducing the fitnesses to dimensionless quantities by redefining them *relative* to fitness of the w_{11} genotype. The percentage advantage or disadvantage can then denoted by the coefficient of selection, s which appeared in an *absolute* context in eqn.(3) above. For example, assuming a multiplicative fitness scheme,

$$W_{11} = \frac{w_{11}}{w_{11}} = 1 \quad W_{12} = \frac{w_{12}}{w_{11}} = 1 - s \quad W_{22} = \frac{w_{22}}{w_{11}} = (1 - s)^2 \quad (7)$$

Plugging these fitness values into eqn. (2), and remembering that $q = 1 - p$, yields after some algebraic manipulation,

$$\Delta p = p' - p = p(1 - p) \frac{s}{1 - s + sp} \quad (8)$$

Thus by introducing relative fitnesses, and retaining all other, albeit ecologically unrealistic assumptions for HW equilibrium, a simple two parameter model of natural selection can be analyzed. The issue of population size and the manner in which fitness is measured, are important issues in the marriage of population biology and population genetics, and will considered in the next section. Furthermore, population geneticists during this period increasingly channeled their efforts towards extending one locus two allele cases towards more genetically realistic multi-locus models involving epistasis and genetic recombination (Provine 2001). For mathematical tractability, this had to be at the cost of ecological reality such as demographic fluctuations and environmental heterogeneity, topics very much at the heart of ecological research.

Evolutionary theory was not entirely oblivious to ecological reality though, and two distinct topics in particular impinged on evolutionary thought. One was demography, the evolutionary importance of which was championed by Elton (1930), and the other was ecological heterogeneity and niche partitioning, on which Gause (1934) did seminal ecological work, and which really came to the fore in evolutionary ecology with Lack's work on the Galapagos finches in the 1940's (Lack 1947). In the "Causes of Evolution" Haldane paid some attention to conjectures by Elton (1930) and other evolutionary-minded ecologists about the role of finite population size and random extinction in evolution, but concluded that these factors had a minor role to play (Haldane 1932, pp. 201-204). By the 1930's, groundwork had been laid for modeling the effects of finite population sizes and spatial heterogeneity (Fisher 1930; Haldane 1932), which was developed further by the succeeding generation of population geneticists using stochastic theory. Wright's "Shifting Balance Theory" for evolution, which invokes both finite population sizes and spatial heterogeneity is perhaps the most ecologically realistic population genetics theory coming from a evolutionary theorist of the period (Wright 1931; Wright 1968).

It is worth noting that by the early 20th century, the two aspects of ecology mentioned at the beginning of Section 2 above, viz., the study of populations, and the study of the relevant environment, were clearly being given different weightage by different scientists in ecology and evolutionary biology. This is discussed further below, and it will be seen in the next section that this fact has had a strong impact on how evolutionary ecology or the synthesis of population biology and genetics is pursued today.

2.3 Marriage and the quest for harmony: 1950-1985

Kingsland (1985, pp. 143-144) observes that there was a widespread disinterest apparent in the activities and views of ecologists and evolutionary biologists towards the other field from the 1920's into the 1950's. From closely entwined origins, ecology and evolutionary biology had diverged in many respects, resulting in deep-rooted cultural differences^{vii}. The historical background above indicates various factors that contributed to the divergence of the two fields. Most of these persist today, and will be considered in more detail in the next section.

263 Around 1950, a renewed awareness of the chasm that had developed between evolutionary biology
264 and ecology arose, with work such as David Lack's research on the Galapagos finches reiterating the
265 importance of ecological heterogeneity, biotic interactions, and niche partitioning (Lack 1947). A shift
266 away from the essentially equilibrium "balance of nature" view also played an important part in this.
267 While a large body of ecologists continued to pursue the program of physical ecology involving detailed
268 studies of the interface between the environment and ecological units ranging from individual to whole
269 ecosystems (Odum 1953; Lotka 1956), the view had become distinctly more dynamic for many others. In
270 part this was due to the publication of the "The Theory of Island Biogeography" by MacArthur and
271 Wilson (1967) which simultaneously introduced two ideas atypical to the ecological thought of that time;
272 a neutral theory of maintenance of communities immigration-extinction dynamics, and a strong synthesis
273 of ecological and evolutionary thought. MacArthur's other work was also very influential, and within a
274 short period of less than two decades, he initiated considerable shifts in the ecological community's
275 viewpoints about theory as well as empirical work (Kingsland 1985). He made many contributions to the
276 theoretical fusion of population genetics and population biology, and had a big impact in drawing the
277 attention of the ecologists towards evolutionary thinking. As Rosenzweig (1987) says, "MacArthur's
278 greatest contribution may have been that he seems to have got through to ecologists that they ignore
279 evolution at the peril of missing the most predictive aspects and beguiling issues in ecology."

280 Additionally, the interface between genetics and ecology was also beginning to be seen as an exciting
281 and important area of theoretical and empirical work as the discovery of the genetic code, and advances in
282 bio-molecular techniques allowed hitherto impossible quantification of genetic variation in nature (Ford
283 1964; Lewontin 1974). This spurred on the efforts to combine models of population genetics and ecology,
284 and the period from 1960 onwards saw frequent appearance of papers, seminars, and books that displayed
285 the intention to bring the theories and practices of ecology and evolution together. These included the
286 works of both, ecological minded evolutionary biologists and vice versa (Ford 1964; Levins 1968;
287 Lewontin 1968; Drake 1968; Riley 1970; Connell, Mertz, and Murdoch 1970; Sammeta and Levins 1970;
288 Dawson and King 1971; Emlen 1973; Lewontin 1974; Cody and Diamond 1975; Karlin and Nevo 1976;
289 Stonehouse and Perrins 1977; Brussard and Allard 1978; Roughgarden 1979; Solbrig and Solbrig 1979;
290 Solbrig 1980; Shorrocks 1984; Wöhrmann and Loeschcke 1984; Strong 1984). The first textbooks
291 explicitly attempting to present an evolutionary ecology perspective also appeared during this period (e.g.,
292 MacArthur and Connell 1966; Pianka 1973; Hedrick 1984).

293 Naturally, these forays into evolutionary ecology reflected the difference in approach of scientists.
294 Introducing the aims and scope of the journal *Evolutionary Ecology*, Rosenzweig (1987) says, "...some
295 of our articles will examine the evolution of natural ecosystems. Others will stress how the external
296 environment, biotic or abiotic, influences the course of evolution. Finally, there will be some that study
297 how the environment actually molds the evolutionary mechanisms themselves." Among these, the most
298 common theme was the role of the abiotic and biotic milieu in guiding evolution, well expressed in
299 Hutchinson's (1965) metaphor of "The ecological theater and the evolutionary play". This focus on
300 ecology as a background for evolutionary processes continues to be a dominant theme in evolutionary
301 ecology (see Section 3)^{viii}. This perceived role for ecology in biological theory will be an important part
302 of the philosophical discussion in the last section.

303 As always, there was a difference in approach between ecologists and evolutionary biologists towards
304 the synthesis. Whereas ecologists focused on evolution with respect to population dynamics, interspecific
305 interactions and environmental aspects external to focal populations (e.g., heterogeneity of the biotic and
306 abiotic habitat), ecologically oriented evolutionary geneticists such as Lewontin and Ford made detailed
307 investigations of genetic variation in nature with a more population genetics approach. The term
308 "Ecological Genetics" was coined by Ford in 1964, a field which in his words, "...deals with the adjustments
309 and adaptations of wild populations to their environment" (Ford 1964). This program was bolstered by further
310 development of population genetics theory on evolution in spatially heterogeneous environments, that had
311 been initially formalized by Wright, Fisher and Haldane (Provine 2001)^{ix}. A significant development
312 during this period, which had a huge impact on the evolutionary ecology synthesis, was the development
313 of quantitative genetics theory (Falconer 1960). Based on Fisher's (Fisher 1930) initial work and the ideas

of the biometrician school of genetics (Provine 2001), this involved modeling evolution of quantitative, polygenic traits without explicit description of the underlying genetics, by using statistical descriptors (e.g., mean & variance) of trait values. This approach was extremely useful from the viewpoint of empirical work, as it generated predictions about expected changes in continuously distributed trait values and indirect measurements of the strength of selection and fitness components from field data. Quantitative genetics therefore quickly became an integral component of ecological genetics.

In a way, quantitative genetics was the ideal middle ground between population genetics and population ecology, as it involved a simplification of certain genetic as well as ecological complexities, yet addressing realistic scenarios. For example, consider a trait value θ , which is continuously distributed in a population as a Gaussian function $p(\theta)$ (i.e., the trait values are assumed to be normally distributed). Assume that there is no gene flow or mutation affecting the character, nor linkage disequilibrium (Slatkin 1980). As before, Let $w(\theta)$ be the absolute fitness of an individual with the a trait in distribution of θ . Various selection models can be can be used to generate values of $w(\theta)$ (see below). Assuming that the $w(\theta)$ functions are given, the change in mean and variance of the trait values are respectively,

$$\bar{z}(t+1) = \frac{\sigma^2}{\sigma^2 + \sigma_e^2} \int \theta p(\theta) w(\theta) \frac{d\theta}{\bar{W}} \quad (9)$$

and

$$\sigma^2(t+1) = h^4 \int [\theta - \bar{\theta}(t)]^2 p(\theta) w(\theta) \frac{d\theta}{\bar{W}} + \left(1 - \frac{\sigma^2}{\sigma^2 + \sigma_e^2}\right) \sigma^2(t) \quad (10)$$

where σ_e is the environmental component of the variance, and $\bar{W} = \int p(\theta) w(\theta) d\theta$. The term $\sigma^2 / \sigma^2 + \sigma_e^2$ is traditionally called the heritability (h^2). Such models can be used to examine the effect of a wide range of selection mechanisms, depending upon what functions are used to define the $w(\theta)$'s. Quantitative genetics circumvented some of the problems faced by previous attempts to model selection under frequency and density dependent population growth (MacArthur 1962; Lewontin 1974)^x, by allowing tractably modeling of continuously distributed traits with definable fitness measures (see below). Its application to modeling niche width, species interactions, character displacement, and niche partitioning had a huge impact on the progress of the evolutionary ecology synthesis in the 1970's (Slatkin 1970; Roughgarden 1972; Slatkin 1979; Slatkin 1980) by creating the first realistic evolutionary versions of hitherto purely demographic models (MacArthur and Levins 1967).

Another important step towards a demographically realistic evolutionary theory was the extension of models of selection to continuously breeding, age-structured populations (Charlesworth 1980). The temporal aspect of environmental heterogeneity and its effect on evolution also received attention during this period from both ecologists as well as evolutionary biologists. The approach again, was rather different, with population biologists tending to use demographically explicit models (Levins 1968) (Slatkin and Lande 1976), whereas population geneticists, following Kimura's neutral theory of molecular evolution (Kimura 1983), focused on genetic polymorphism, using stochastic theory to address questions of evolution under fluctuating selection by building on preliminary work by Haldane and Jayakar (1963; cf. Gillespie 1991). The idea of temporally fluctuating environments was also central to the development of theory on the evolution of sex (Maynard Smith 1978).

However, along with this upsurge of exchange between ecology and evolutionary biology from the 1950's onwards, other issues within the two disciplines increasingly claimed attention, contributing further to the overall divergence of the two. Evolutionary biologists on one hand, enthused by advances in molecular biology were increasingly caught up in the gene-centered view of life, which was essentially reductionist (Sarkar 1998). Apart from the different ways, as mentioned above, in which ecological realism was brought in by population geneticists into their models, a large body of biologists delved

deeper into genic models of selection and evolution, ignoring many aspects of genotype environment relationships. This reductionism has been lamented as being one of the causes of disunity between population biology and population genetics (Levins 1968; Ayala and Dobzhansky 1974; Levins 2004).

In ecology on the other hand, debates raged over the nature of community assembly, measures of stability in biological systems, the relative role of extrinsic vs. intrinsic factors driving ecological dynamics, the relationship between species diversity and community stability, the role of history in ecological patterns, and importance of processes at different spatial scales in determining diversity. Along the way, ecological sub-disciplines multiplied, with the addition of fields such as metapopulation ecology, metacommunity ecology, spatial ecology and landscape ecology. Unlike in evolutionary biology, a large rift also developed between theory and empirical work, with field biologists finding it tough going to glean testable predictions from complex, mechanistic models often inspired by physics, raising deep philosophical concerns about the role of theory in ecology and the place of ecology in biology (Kingsland 1985; Kareiva 1989; Sterelny and Griffiths 1999). Field ecology became increasingly preoccupied with conducting detailed characterizations of ecological patterns from at various levels of complexity ranging from individuals to ecosystems. The hope was that cataloguing patterns and processes would somehow reveal general principles. This was the period when global patterns such as “Rapoport’s rule” (Gaston, Blackburn, and Spicer 1998) and “Bergmann’s rule” (Freckleton, Harvey, and Pagel 2003) were described. A formidable array of statistical techniques were also developed during this period to allow a mechanistic characterization of organism environment interrelationships. Evolutionary ecology took somewhat of a back-seat in these pursuits; especially because apart from a few exceptions, most of the focal biological systems for empirical work were vertebrates, where the role of evolution was considered insignificant at ecological time scales. Instead, complexity of the systems being studied commanded almost complete attention.

Nevertheless, in the mean time the unification of population genetics and population biology continued by a small group of biologists. From the 1980’s onwards in particular, the effort came closer to achieving a more seamless union due to the use increasingly sophisticated mathematical treatment and careful empirical testing with new model systems by a new breed of biologists who dwelt comfortably in both ecological and evolutionary hemispheres. In particular, the convergence of multilocus population genetic and quantitative genetic models (Bürger 2000) allowed greater ecological flexibility as well as genetic reality to evolutionary ecology modeling (e.g., Doebeli 1996a; Doebeli 1996c). In the process, these efforts diversified into various distinct approaches, which will be considered in the following section.

3. THE MARRIAGE OF ECOLOGY AND EVOLUTIONARY BIOLOGY: THE UPS, THE DOWNS, AND A TAXONOMY

I will now attempt a classification of contemporary approaches in evolutionary ecology, based on three themes that appear to have traditionally been at the core of dissent between ecology and evolutionary biology: the issue of time-scale, the role of demography, and the effect of environmental heterogeneity. I will discuss these before presenting and discussing the classification. Of the three topics to be discussed, “time-scale” is mainly a cultural issue, referring to the importance given to history in population biology. Although there is no definable boundary between micro- vs. macro- evolutionary, or ecological vs. evolutionary time scales, the question of relative importance of processes at different time scales have generated distinct disciplines and this issue has apparently been a key factor affecting the unification of ecology and evolutionary biology.

The other two criteria are conceptual. The issue of demography is closely tied to the concept of fitness, and the two will be discussed together. Richard Levins gave a succinct account of these conceptual issues more than forty years ago, during an early phase of the evolutionary ecology synthesis (Levins 1968, p. 5; the focal topics are underlined): “ ‘Darwinian fitness (Wright’s \bar{W}) has to be interpreted in terms of its ecological components, such as the intrinsic capacity for increase (Andrewartha and Birch’s r_0) and the carrying capacity of the environment for a given genotype (K).’ ... ‘While the

population geneticist's models generally assume stable age distributions, fixed populations sizes, and constant environments in order to study the pattern of genetic heterogeneity in single species, the population ecologist considers genetically uniform populations in multispecies systems in a heterogeneous environment' ”.

3.1 The issue of “ecological vs. evolutionary time scales”

As mentioned above, the early school of evolutionary thought was essentially gradualist, with a firm belief in the slow and steady progress of evolution over the geological time scale, a view point that is still prevalent (Stanley 1989). A competing view of punctuated equilibrium too exists, but this does not alter the argument that is being made here. The relevance of micro-evolutionary processes to observed macroevolutionary patterns, is still an contentious issue in evolutionary biology because of the observed opposition of trends at different time scales (Stanley 1989; Bennett 1997). As such, this issue does not affect the evolutionary ecology synthesis much because evolutionary biologists naturally emphasize lineage-dependent processes and incorporate them into microevolutionary studies in an ecological context. However, a related view in ecology, that ecological and evolutionary time scales are independent of each other, has had considerable influence on the importance given to evolutionary processes in ecology. Tied to this is the strong faith among many ecologists of the existence of adaptation and co-adaptation in natural populations and their persistence over long, geologically significant periods of time (Hubbell 2001). For example Pimm (1991) discusses the stability and persistence of populations with respect to time scales ranging from centuries to millennia or more, invoking evolution only as a purely historical process. Similarly, Tokeshi (1999) discusses evolution in community structure on purely geological time scales. These perspectives naturally result in omission of evolutionary thought from ecological research. I have already mentioned above that a view of disjunct temporal processes is rooted in the tradition in biology to study a small set of vertebrate model systems (Bonnet, Shine, and Lourdaïs 2002).

There is no denying that evolutionary history is an important factor to consider in ecology, and has been given due consideration. However, the role of microevolution in ecological patterns and processes has not been well evaluated. In the last two decades or so, ecological geneticists and molecular ecologists have shown ample evidence for the existence of functional polymorphism and gene frequency shifts in nature. Not surprisingly, there is now an increasing awareness of the need to integrate macro- and microevolutionary processes in ecology at different scales of organization (Cavender-Bares and Wilczek 2003). In addition, the use of microbial model systems in ecology has also allowed many ecological questions to be answered in an evolutionary context, often adding important insights relevant to other systems where such methods not possible (Jessup et al. 2004). Perhaps ironically, the empirical insights from contemporary microbial work have come more than 60 years after Gause's (1934) ecological experiments with microorganisms, which too had a strong evolutionary context. No doubt advances in laboratory molecular biology techniques have a large part to play in this, but this also reflects the reticence of ecologists to deviate from established model biological systems.

The argument here of course, is not that research on elephants and tigers be completely abandoned in favor of laboratory cultures; it is a plea for a pluralism of empirical approach that will provide insights for finding avenues of escape from the theoretical cul-de-sac that ecologists often find themselves due to the inability to test crucial aspects of their models (Kareiva 1989). Indeed, in the subsequent discussion on the empirical support for evolutionary ecology theory, there will be a striking preponderance of work on rapidly evolving model organisms such as bacteria and *Drosophila* that have provided new insights into questions that have traditionally challenged ecologists.

3.2 Demographic considerations and measures of fitness

From a population biology perspective, many questions are raised by the treatment of demography and the closely tied concept of fitness in evolutionary biology. The issue of fitness in particular, is a

controversial one even within evolutionary biology (Ariew and Lewontin 2004; Lewontin 2004). For the purposes of this paper however, I will focus on three aspects of population genetics that have particularly troubled population ecologists. The first two of these are visible in the illustration of the traditional population genetics approach in eqns.(2-8) above. The problems are, (i) population sizes are assumed to be infinite, which circumvents the complications of random birth-death processes in finite populations (called ecological drift or demographic stochasticity; cf. Hubbell 2001), (ii) The Malthusian parameter r is converted into a fitness measure s by assuming fixed population size, which allows the convenience of reducing the parameters to just genotype proportions and relative fitnesses, and (iii) When considering inter-specific interactions, the mean fitness (see eqn.(4)) of species' population becomes an absolute measure, creating the need to develop a general algorithm for translating absolute fitnesses between populations. As will be emphasized below, the use of quantitative genetic models helped resolve the problem theoretically, but the practicability of measuring fitness components in the field remain a difficult issue.

The issue of infinite population size was dealt with by population geneticists by introducing population size as a statistical parameter that affected the rate of random genetic drift— effective population size, N_e (Kimura 1983). Although it was not an entirely satisfactory solution from a population biology perspective as it is only a phenomenological model of demographic stochasticity, it was acceptable in ecology because it could still be used to consider the evolutionary consequences of finite population size in terms of extinction probabilities (Caughley 1994). The issue of fixed population sizes on the other hand, raised some crucial questions for population biologists. What happens when populations change in size as they inevitably do? Or when generations are not discrete, but overlapping? Or when population change is density dependent? Extensions of population genetics theory to address questions of population change and overlapping generations had been accomplished by the 1970's, albeit with some issues still unresolved (Charlesworth 1980; Lewontin 2004).

Evolution under density dependent population growth were first modeled by Kostitzin (between 1935-40; op. cit. Christiansen 2004), and (Fisher 1930) by assuming weak selection, and fitnesses dependent upon density dependent death rates. Subsequently, (MacArthur 1962) used a similar approach, but used the then familiar r & K parameterization of the Pearl-Verhulst logistic growth equation of density dependent growth,

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) \quad (11)$$

This general approach, which was developed further by others (Christiansen 2004) will be briefly illustrated here. Consider a haploid, asexual population with only two alleles 1 & 2 at a single locus. Assuming that the population is under density dependent growth, the fitnesses can then be defined as (cf eqns 2-3),

$$w_1 = 1 + r_1 \left(1 - \frac{N}{K} \right) \quad \& \quad w_2 = 1 + r_2 \left(1 - \frac{N}{K} \right) \quad (12)$$

Frequency dependent selection and genotype-specific carrying capacities can now be included by extending eqns 12 to,

$$w_1 = 1 + r_1 \left(1 - \frac{N_1 + N_2}{K_1} \right) \quad \& \quad w_2 = 1 + r_2 \left(1 - \frac{N_1 + N_2}{K_2} \right) \quad (13)$$

which amounts to rephrasing the Lotka-Volterra equations (eqns. (1)) for competition of two species to competition between two genotypes of one species, assuming the intra-specific competition parameters to be $\alpha_{12} = \alpha_{21} = 1$. Extensions of such models to overlapping generations under different single-population scenarios, as well as to coevolution of two or more species have provided many interesting insights, and

contributed to the unification of population genetics and ecology (Christiansen 2004). The first major result of this research of course, was the development in the 1970's of the ideas *r-K* selection and the role of the environment in shaping life history strategies (MacArthur and Wilson 1967; Roughgarden 1996; Christiansen 2004).

However, modeling fitnesses under frequency as well as density dependent growth in multiple populations does create the third problem mentioned above: that of absolute fitnesses. The interpretation of density dependent fitnesses becomes difficult in multi-species systems because mapping the effect of each populations absolute mean fitness on another population becomes context dependent because fitnesses are a function of the environment under this scheme (because they are tied to *K*), instead of being an inherent property of individuals' genotype (Ariew and Lewontin 2004; Lewontin 2004). This makes it difficult to develop a framework for making general predictions about the evolutionary outcomes of species interactions without taking the situation-specific environment-phenotype-genotype map into consideration. For example, if we want to extend eqns.(13) to two haploid asexual species *A* & *B*, each experiencing intra- and inter-specific density as well as frequency dependent selection, we could begin with, assuming one locus and two alleles, and using the Lotka-Volterra scheme,

$$w_{1A} = 1 + r_{1A} - \frac{r_{1A}}{K_{1A}} N_A - \frac{r_{1A}}{K_{1A}} (\alpha_{1A1B} N_{1B} + \alpha_{1A2B} N_{2B})$$

$$= 1 + r_{1A} - \frac{r_{1A}}{K_{1A}} [N_A - (\alpha_{1A1B} p_B + \alpha_{1A2B} (1 - p_B)) N_B]$$

and similarly,

$$w_{2A} = 1 + r_{2A} - \frac{r_{2A}}{K_{2A}} [N_A - (\alpha_{2A1B} p_B + \alpha_{2A2B} (1 - p_B)) N_B],$$

where w_{1A} and w_{2A} are as before, the fitnesses of the two genotypes, while r_{1A} , r_{2A} & K_{1A} , K_{2A} are the genotype-specific intrinsic rate of increase and carrying capacity respectively. This model assumes that a genotype in a species *A* interacts with all available genotypes of species *B* in the community in proportion to their frequency. Thus, α_{1A1B} and α_{1A2B} represent the competition coefficients of genotype 1 in species *A* with genotype 1 and 2 in species *B*, respectively. These are multiplied by the frequency of the respective genotype (p , $1 - p$). The competition coefficient introduces the effect of interspecific frequency dependence relative to intraspecific density dependence (MacArthur 1972; Laska and Wootton 1998). If α were zero, the interacting populations would experience purely intra-specific density dependent growth and selection. Rewriting eqn. (4) in terms of eqns. (12&13) gives the mean fitness of the population:

$$\bar{W}_A = 1 + \bar{r}_A - \frac{\bar{r}_A}{\bar{K}_A} (N_A - \bar{\alpha}_{AB} N_B),$$

where

$$\bar{r}_A = p_A r_{1A} + (1 - p_A) r_{2A},$$

$$\frac{\bar{r}_A}{\bar{K}_A} = p_A \frac{r_{1A}}{K_{1A}} + (1 - p_A) \frac{r_{2A}}{K_{2A}},$$

and

$$\bar{\alpha}_{AB} = \alpha_{1A1B} p_B + \alpha_{1A2B} (1 - p_B) + \alpha_{2A1B} p_B + \alpha_{2A2B} (1 - p_B)$$

In each generation, the population growth is a function of the mean fitness \bar{W}_i of the population in the previous generation, made up of the relative contributions of the two genotypes. For example, if allele A is fixed in the species A, its population will grow at a density dependent growth determined by the r and K values of the genotype 1A and its interaction with genotypes of species B. Eqns.(14-19) illustrate the difficulty with measuring fitness in such situations. In this model, one would have to keep track of no less than 10 parameters to evaluate the evolutionary outcome of interaction between just two species! And this is assuming that α is a reasonable representation of both direct and indirect interactions in nature.

Computer simulations and mathematical analyses (with some reparameterization) of these models do yield insights, but measuring all the components of fitness in such a situation to be an almost impossible task in reality, let alone defining a more general scheme for translating absolute fitnesses between species.

The problem is considerably simplified by using a quantitative genetics framework (see eqns. (9-10) above). For example, for the two competing species in the above example, the fitness functions from eqns (14 & 16) could be easily modified to feed into eqns. (9 & 10), thus creating a quantitative map between fitnesses of the two populations generated by frequency- and density-dependent interactions within and between species. However, the empirical problem of measuring all the components of fitness still remains a difficult issue. On the whole then, the manner in which fitnesses are dealt with will be an important criterion for the classification presented below. It will become apparent that certain model systems that have been used in recent empirical work are relatively amenable to estimation of fitness components, and this has gone a long way in testing some theoretical predictions.

It should also be noted that in addition to examining the role of demography in evolution, it is possible to flip the question over, and focus on the effects of evolution on population dynamics. Such work has also emerged in recent years and is an area of active theoretical development and empirical research, adding yet another facet to evolutionary ecology.

3.3 The role of environmental heterogeneity

The ‘problem’ of complex population behavior and the role of “external” vs. “internal” factors plays an important role in ecology (Hastings et al. 1993). In search for answers to such questions, ecologists have expended considerable effort over the last century for a detailed characterization of heterogeneity in nature. Areas such as landscape and spatial ecology have steadily built a realistic characterization of heterogeneity in nature, and to many biologists, ecology is synonymous with environmental characteristics; the ecology of a species is at least as likely to connote the organism’s environment as its inherent properties, such as life history characteristics. As was pointed out above, the area of ecological genetics has developed around this view of ecology.

The incorporation of environmental heterogeneity into a unified evolutionary ecology framework is far from complete though. This is one area where the flow of information must largely be from the direction of ecology (in its environmental avatar) towards evolution. As Levins (2004) points out, “‘There has always been a much finer sophistication of our understanding of genetic variation than of the environment,’ ‘...a successful study of evolution requires the recognition of the complexity, not just of the genotype, but also of the environment and of the whole organism in its development and its physiological flux’ ”. This is of course, a reiteration of the argument made above about the effect of genetic reductionism on the conceptual unification of population genetics and population biology. Practitioners of ecological genetics do indeed often pay just lip service to environmental heterogeneity, using a set approach of employing statistical tools to fit observed genetic variation to predictions of traditional population genetics models, most of which have tenuous connections with ecological reality. Statistically reasonable fits may be observed, but the results do not reveal whether the model being tested describes the real mechanisms for the maintenance of genetic variation. Although this is general concern in all scientific disciplines, it is also a function of how much of the universe of possibilities has been explored while formulating theories.

In the quest for a formal description of all the nuances of environment complexity, ecologists have been no laggards; the mathematical structure of many aspects of the environment in which evolution can potentially operate has been well characterized in both time (e.g., Vasseur and Yodzis 2004) and space (e.g., Keitt et al. 2002). For example, consider Figure 1, which shows an empirical observation of temporal environmental pattern: seasonal variation in temperature across latitudes. It is well known that the amplitude of seasonal cycles as well as random environmental noise increases away from the latitudes (Vasseur and Yodzis 2004).

This observation is easily translated into a model of fluctuating selection (cf. Bürger and Gimelfarb 2002). Consider a selectively optimum trait value θ , such as the one introduced in eqn.(9). Assume that the position of the optimum fluctuates cyclically about the midpoint of the range of trait values (θ_o), with a scaled random perturbation around it. This can be modeled by assuming that at time t the optimum θ_t is drawn from a normal distribution with mean

$$\theta_t = \theta_o + A \sin\left(\frac{2\pi t}{L}\right) \quad (20)$$

where A is the amplitude and L the length of the selection cycle relative to the organism's generation time. The perturbations have a standard deviation $\sigma_\theta = dA$, where d is a measure of the magnitude of stochasticity. If $d=0$, there is purely cyclical selection; if, in addition, $A=0$, there is pure Gaussian stabilizing selection. Figure 2 shows the temporal pattern of cyclical selection generated from this model with arbitrary parameter values. This matches the empirical pattern in Figure 1 quite well.

This idea can then be further developed to consider the effect of such environmental grain on evolution as well as persistence of populations. After the initial beginning in the 1960's of work on the effect of fluctuating environments on adaptation and persistence of populations, the role of periodic instead of completely random fluctuations, partly motivated by empirical patterns like the one in Figure 1, increasingly drew attention over the last decade or so, yielding new insights (Lande and Shannon 1996; Kirzhner, Korol, and Nevo 1998; Bürger and Gimelfarb 2002; Wichmann et al. 2003). Detailed examination of such empirical patterns of environmental heterogeneity can also help resolve questions about the likelihood of seeing certain evolutionary processes in nature. For example, Gillespie {Gillespie, 2004 5521 /id /d} has long argued that widely accepted population genetic models of adaptive evolution in DNA sequences need to be reevaluated in light of the fact that certain patterns of fluctuating selection can generate patterns of polymorphism akin to those from models of neutral evolution, a claim that remains largely untested. The evolutionary ecology synthesis will definitely benefit from the use of environmental information; the extent to which this has been achieved is considered in the classification that follows.

3.4 A Taxonomy of evolutionary ecology

A classification the contemporary approaches that combine ecological and evolutionary perspectives from population genetics and population biology are presented in Table 1. Keeping then tradition initiated by stalwarts of the evolutionary ecology synthesis, I drop the term "evolutionary ecology" in favor of "population biology" for this classification (Lewontin 2004; Levins 2004) /pt "cf. ";(Travis and Mueller 1989).

Each of these research programs is now discussed with reference to the nature of scientific approach, the conceptual issues it addresses, its theory and supporting empirical data. Together, these disciplines comprise a number of research topics and a huge body of literature, and this discussion below does not claim to be an exhaustive survey of all topics. Within each research program however, poorly explored avenues of interesting research are also mentioned.

I. Paleo-population biology

One solution towards fusing evolution and ecology is to incorporate historical processes by reconstructing the evolutionary history and paleo-ecology of populations and drawing inferences about contemporary properties of organisms. Two distinct approaches are currently being used:

(a) *Non-demographic schema*

Approach. This program of research is an outcome of the above-mentioned ‘historical’ viewpoint mentioned that has been so prevalent in ecology. This program was invigorated in the 1990’s by the introduction of phylogenetic techniques, thus allowing a more reliable reconstruction of evolutionary history (Eggleton and Vane-Wright 1994; Losos 1996). This method is non-demographic in the sense that population size considerations rarely enter the analyses, either in the historical reconstructions, or in the study of contemporary adaptations. The concepts of fitness used here are absolute and qualitative, with the outcome of interactions between populations described in terms of the apparent level of fitness in populations.

Research themes: *theory and empirical results.* This approach is strongly retrospective, generally involving verbal extensions of prospective evolutionary ecology models such as those of character displacement and the mapping of traits onto phylogenies (Eggleton and Vane-Wright 1994; Losos 1996). Some prominent themes for research are adaptive radiation into ecological niches (Schluter 2000; Losos and Miles 2002), Outcome of species interactions (e.g., evolutionary character displacement; (Radtkey, Fallon, and Case 1997), and the manner of community assembly (Gillespie 2004b). The insights from these lines of work have served to greatly clarify the role of evolution in structuring communities and molding species interactions. For example, Gillespie (2004b) has shown that convergent evolution into similar niches has an important role in community assembly, shedding light on the long unresolved debate in community ecology about the manner of community assembly, and the existence of “assembly rules”(Weiher and Keddy 1995). On the flipside, such studies contribute a lot towards clarifying the role of ecology in speciation, a burgeoning topic in evolutionary biology (Coyne and Orr 2004).

(b) *Demographic schema*

Approach. This relatively new area involves the inference of “historical demography” combined with analyses of properties of extant populations. This has been made possible by recent attempts to bring the coalescent theory (Kingman 2000) of population genetics and phylogenetics closer together to evaluate the interrelationships between micro- and macroevolution (Wakeley 2004). This approach also opens up the possibility of explicitly including historical population structure in analyses of current populations, a topic that has hitherto been difficult to deal with except by verbal arguments in ecology as well as evolutionary biology. As paleo-population structure is inferred purely from nucleotide polymorphism data, this approach obviously cannot infer past environmental heterogeneity explicitly unless paleo-ecological events can be dated and implicated using molecular clock approaches. Fitnesses obviously do not even enter the picture as far as the historical component is concerned. The analyses of extant populations of course can of course include both, fitness measures and consideration of environmental heterogeneity.

Research themes: *theory and empirical results.* Obviously, the past can impinge upon almost every feature of extant organisms. The themes that will be developed in this area will only be bound by the limits of the collaboration between paleobiology, phylogenetics, coalescent theory, and ecology. These are widely separated disciplines, and a coherent theory will probably take a while to develop. Research in this area could include, but need not be restricted to, all of the themes of the approaches under the non-demographic schema mentioned above. For example, recently, Flanagan et al (2004) used such an approach to clarify the role of historical demography in the coevolution of two Müllerian comimetic

butterfly species. The potential of this area of research is huge all the questions asked in the non-demographic schema above can be better addressed by such analyses.

II. Microevolutionary ecology

This is a much larger area of research than paleo-population biology, because prospective study of extant populations is the predominant approach in population biology. This area involves the consideration of microevolutionary changes in generating ecological patterns and processes, as well as the effect of the environment on observable evolution. Two broad categories of approach can be identified here:

(a) *Non-demographic schema*

Approach. This program involves the extension of population genetics (including quantitative genetics) to realistic ecological (in the sense of the adaptive environment) scenarios, for a detailed examination of populations' characteristics in relation to the environment. In keeping with the population genetic framework, population size only appears if at all, as N_e , and fitnesses are relative, or if multiple species are considered, may be juxtaposed by analyses of mean population fitnesses (generally using quantitative genetics). The most common aspect of ecological heterogeneity is spatial, while temporal variation in the abiotic environment is increasingly being studied, with rare examples of a combination of the two (Frank and Slatkin 1990).

Research themes: *theory and empirical results.* Most studies in ecological genetics and molecular ecology use this approach to establish the relationships between genetic variation in nature and ecological heterogeneity (Charlesworth, Charlesworth, and Barton 2003), wherein the focal population's environs can be both biotic (e.g., herbivore-plant interactions), as well as abiotic (DeSalle and Schierwater 1998; Beebe and Rowe 2004; Conner and Hartl 2004). Other themes are evolution in temporally fluctuating environments (Gillespie 1991; Sasaki and Ellner 1995; Ellner and Sasaki 1996; e.g., Sasaki and Ellner 1997), evolution in spatio-temporally fluctuating environments (Frank and Slatkin 1990), evolutionary outcome of species interactions with such as competition and predation with or without interactions with the environment (Slatkin 1979; Slatkin 1980; Abrams 2000; Antonovics 2003). A large empirical area corresponding to the last is the whole area of evolutionary ecology of plant-animal interactions, which involves the study of coevolution between populations, which does not generally consider demography explicitly, defines fitnesses largely qualitatively in terms of apparent adaptations of populations, with or without consideration of abiotic environment (Drake 1968; Emlen 1973; Karlin and Nevo 1976; e.g., Wöhrmann and Loeschcke 1984; Beattie 1985; Price 1991; Poulin 1998). An important area that has recently come to the fore is the study of the role of the environment in determining evolutionary rates at the molecular level (Pawar 2005). This has raised some interesting new questions about the evolutionary mechanisms behind latitudinal diversity gradients, an issue that has traditionally been an ecological topic. In addition, work with microorganisms has also provided valuable data for evolution in temporally fluctuating (Bell 1997; Reboud and Bell 1997; Scheiner and Yampolsky 1998; Kassen and Bell 1998) as well as spatially variable (Travisano and Rainey 2000) environments.

(b) *Indirect-demographic schema*

Approach. This area involves the study of populations in nature using ecological genetic techniques, and inferring demographic characteristics (generally, effective population size, N_e) indirectly, by using population genetics theory. Fitness measures are absolute, and generally qualitative. Ecological heterogeneity if considered is generally spatial.

Research themes: *theory and empirical results—*

The theoretical basis for this line of research is traditional population genetics theory, where genetic variation is used to estimate demographic characteristics such as N_e and population structure (Hedrick 1984). As most inferences about population characteristics are indirectly inferred, this area has restricted range of themes, and will probably be absorbed into one or more of the other categories. Most results in this area have yielded insights into the impact of natural or anthropogenic environment variation on characteristics of single populations (e.g., Crawford 2003; Woolfit and Bromham 2003; Sumner et al. 2004).

(b) Direct-Demographic schema

Approach. This area of research is a rapidly growing area, and includes a range of distinct research themes that have their origins in ecology or evolutionary biology. All these involve explicit consideration of demography, and the most complex topics involve a three-way interaction between the environment, demographic dynamics, and evolution, perhaps capturing the essence of what has been visualized to be a unified population biology (Roughgarden, May, and Levin 1989; Singh and Uyenoyama 2004). The characterization of fitnesses in this diverse area of research is naturally variable, and to a great extent, the problems that have been mentioned above with the measurement of fitness components is perhaps the most relevant to demographically-oriented objectives of these studies.

Research themes: theory and empirical results. The theory that underlies this area as been covered in parts in the previous sections, and involve demographically explicit models that combine population genetics (including quantitative genetics) with different levels of ecological heterogeneity. The themes of research are wide ranging (cf. Brussard and Allard 1978) include the effects of evolutionary change on demographic characteristics and vice versa (Doebeli and Koella 1994; Doebeli and Koella 1995; Doebeli and Koella 1996; Doebeli 1996b), evolutionary changes in communities (Norberg et al. 2001), evolution of population stability, evolution of life history traits (Levins 1968; Charlesworth 1980; Bradshaw 1984; Charlesworth 1993; Doebeli and Koella 1995; Doebeli 1996b; Doebeli and de Jong 1999; Mueller and Joshi 2000; Mueller, Joshi, and Borash 2000; Norberg et al. 2001; Reznick, Bryant, and Bashey 2002), and evolution in fluctuating environments (Mueller and Joshi 2000; Mueller, Joshi, and Borash 2000; Reznick, Bryant, and Bashey 2002).

This area has had a long history of disjunction between theory and the empirical work, partly because many of the predictions of microevolutionary ecology models cannot be tested easily either because fitness components are difficult to measure, or the rate of evolution in the model organisms is too slow to be observed in reasonable time scales. However, the inclusion of new model systems, which was mentioned at in section 3.1 above, has had a big impact on this situation. For example, work with *Drosophila* and *Poecilia* (Mueller and Joshi 2000; Mueller, Joshi, and Borash 2000; Reznick, Bryant, and Bashey 2002) has produced the first concrete support for some of the predictions of theory on evolution of life history traits. Work with microorganisms too has provided strong evidence for the role of evolution in molding population dynamics (Yoshida et al. 2003; Fussmann, Ellner, and Hairston 2003). This has important implications for the one of the longest-lived problems in ecology of pinpointing the factors driving population cycles in microtine rodents and their predators, for which evolutionary hypotheses had been proposed before, but had received little attention by ecologists (Chitty 1996; Turchin 2003). A number of equally valuable insights on other ecological questions from work with other microorganisms (Jessup et al. 2004).

5. CONCLUSION

5.1 Has The Marriage Come Of Age?

So what has been the outcome of this intricate branching of evolutionary ecology? In a recent paper, Lewontin and Levins, two key figures in the program for a unified population biology, provide an

assessment, which ranges from being cautiously optimistic to rather dyspeptic (Singh and Uyenoyama 2004). After a discussing a range of topics that are at the heart of the synthesis, Levins laments that “This program for an integrated population biology remains an aspiration that has not been carried out in practice. Instead, we see a gross imbalance among these components and a continued separation of the disciplines”. This is definitely true to the extent that the mainstream of ecology and evolutionary biology do indeed proceed happily along a divergent (or parallel) path, as was observed at the beginning of this paper. However, I am inclined to be more optimistic that Levins is.

The taxonomy of a unified population biology that has been presented here is no doubt temporary, but serves the purpose of demonstrating the impressive range of topics that studies undertaking an evolutionary approach have managed to cover, both in theory, and empirical work. One factor that Lewontin and Levins do not seem to have considered, is the crucial role that the quantitative genetics models have played in providing at the very least, heuristic insights into the role of ecology in evolution, and vice versa. Moreover, there is ample evidence for the bi-directional flow of contribution, which indicates a greater balance, perhaps not yet full appreciated, in the nature of the unification. There is no doubt that the marriage has no yet come of age; however, its rapid progress in the last two decades or so, bode good tidings for the not too distant near future.

5. 2 On the Dullness of Ecology

It was pointed out at the beginning that the philosophy of biology appears to suffer from a considerable disinterest in ecology, especially in comparison to evolutionary biology (Hull 1974; Sober 1993; Hull and Ruse 1998; e.g., Grene and Depew 2004). To some extent, this is understandable, as no other work in history has shaken the teleological foundations of human culture, as Darwin’s radical theory (Hull 1974; Sober 1993). Considering the fact that the role of teleology in evolutionary biology have been an important topic of discussion (Sterelny and Griffiths 1999)^{xi}, this disinterest in the philosophy of ecology is surprising because there had been a widespread belief in ecology of the existence of optimal strategies, stability and persistence, the roots and implications of which are worth contemplating about. In this context, Hull (Hull 1974) has a definition of teleology in the biological context that applies well to ecology: “prevalence of preferred states, closed feedback loops and programs, and the origin of such systems by means of selection processes.” On the other hand, apart from the issue of teleology, evolutionary biology also offers a much more coherent theoretical structure compared to ecology, and has thrown up its share of interesting topics ranging from the role of biological determinism, to issues such as the meaning of species, units of evolution and selection, and so on (Sterelny and Griffiths 1999; Grene and Depew 2004).

This paper offers another, perhaps more fundamental reason for a reconsideration of the dullness of ecology. The question of the existence of laws in biology of has been a topic that has troubled biologists and philosophers for a while, and still provides ample fodder for rumination (Kingsland 1985; Bergandi and Blandin 1998; Haila and Taylor 2001; Cooper 2003; Ginzburg and Colyvan 2004). And if philosophers are interested in the laws of biology, where better to look than at the rather discordant structure of ecology? Opinions about the validity of the theoretical foundations of ecology and the presence of laws vary widely, ranging from agreement about the presence of general principles at one end (Turchin 2002; Berryman 2003), to the declaration of the theoretical redundancy of ecology to the advancement of biology on the other (Haila and Taylor 2001). Writing about the relationship between ecology and evolution, Sterelny and Griffiths (Sterelny and Griffiths 1999) invoke Sober’s (Sober 1993) distinction between “source laws” and “consequence laws”. Source laws explain the origins of fitness differences, whereas consequence laws explain the actual evolutionary outcome of these differences. Sterelny and Griffiths judge that the role of ecology is to define the source laws in evolutionary biology.

However, I claim that the results of this paper indicate that this conclusion is incorrect, given the balanced nature of the current collaboration between ecology and evolutionary biology. Ecology and evolutionary biology have clearly made reciprocal contributions to the conceptual advancement of each other. Thus While some may consider the future of ecology as a whole to lie in a stronger integration into

the human social context (Kingsland 1985, pp 65-66; Haila and Levins 1992; Haila and Taylor 2001; Bradshaw and Bekoff 2001), the progress of the evolutionary ecology synthesis suggests that while parts of ecology might indeed have a important social role, a large part of ecology might actually come to rest in an synthetic theory that comprises a more sturdy theoretical foundation than either discipline alone. Neither discipline is theoretically redundant either to each other, or to biology as a whole. While the existence of laws in biology is an important issue, it is perhaps time to consider the theoretical and philosophical implications of the ongoing reunification the two disciplines that were born together with Darwin's theory, which marks the birth of modern biology itself.

Acknowledgements

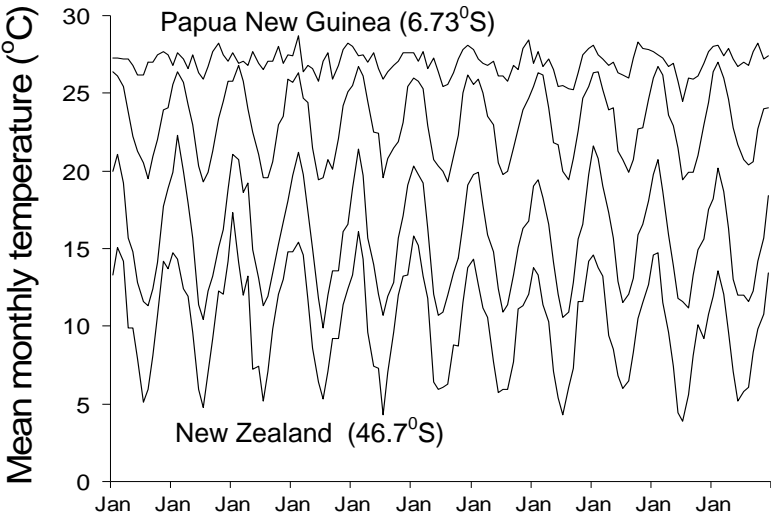
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References

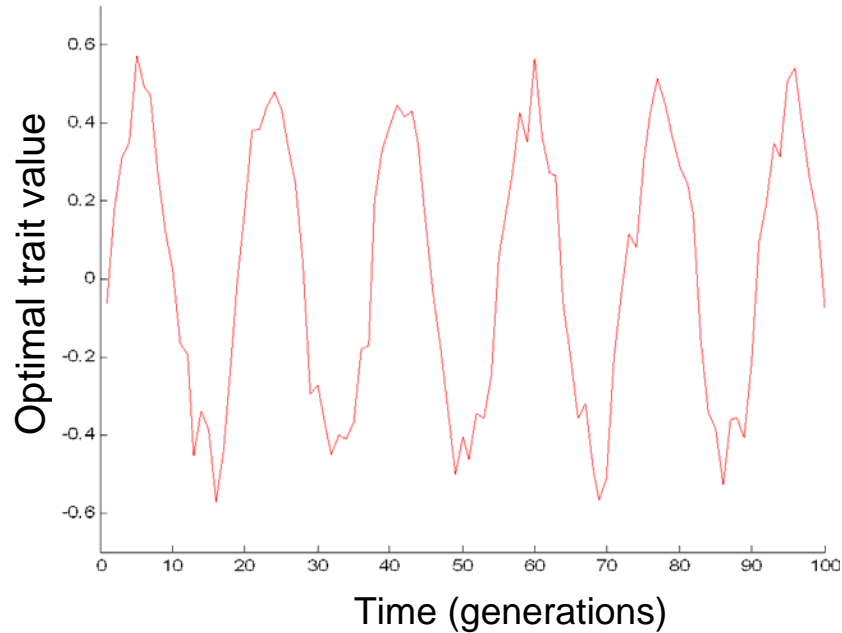
Table 1. A taxonomy of research that unifies ecological and evolutionary perspectives in biology. The issues considered for classification are: approach towards time-scale, demographic considerations, fitness measures, and treatment of ecological heterogeneity.

Category	Scientific approach
I. Paleo-population biology	<i>Retrospective studies considering historical effects on properties of current populations.</i>
(a) Non-demographic schema	Reconstruction of evolutionary relationships without paleo-demographic inferences, with focus on extant populations of two or more species. Fitnesses concepts used are absolute and often qualitative. Structural or spatial aspects of habitat interpretable as niches play an important part.
(b) Demographic schema	Reconstruction of phylogenies as well as gene genealogies with paleo-demographic and paleo-ecological inferences with focus on one or more extant species' populations. Fitness measures and ecological heterogeneity can be considered only in extant populations.
II. Population biology	<i>Essentially prospective studies restricted to "microevolutionary" or "ecological" time scales.</i>
(a) Non-demographic schema	Study of populations without explicit consideration of demography, using traditional population genetic tools. Relative fitnesses are used, assuming fixed population sizes. Ecological heterogeneity, if considered, can be spatial and/or temporal.
(b) Indirect-demographic schema	Study of populations with inference of demographic characteristics (in general, population size), indirectly, by using population genetics theory to estimate N_e . Fitness measures are absolute, and generally qualitative. Ecological heterogeneity id considered, is generally spatial.
(c) Demographic schema	Entail explicit consideration of the interplay between evolutionary changes and demography of populations. Fitness measures vary, often involving density as well as frequency dependence, or are absolute. Ecological heterogeneity, if considered, can be spatial and/or temporal.

Fig. 1. Variation in temperature across months over 11 years for four sites spanning 40° of latitude, from New Zealand (46.7°S), to Papua New Guinea (6.73°S). All sites are from a similar altitude (0–20m above sea level; data from http://bonnet19.cs.qc.edu:7778/pls/rschdata/rd_start.main). Note that the fluctuations increase away from the equator.



884 Fig. 2. Cyclical selection with random fluctuations over 100 generations, based on the model in eqn. (20).
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ⁱ It is an important but difficult proposition to evaluate the success of such endeavors; that issue will not be dealt with here.

ⁱⁱ In doing so, for reasons of brevity many significant figures and interesting details will necessarily have to be glossed over, and the focus will, perhaps a tad unfairly, be polarized towards developments in the United States of America.

ⁱⁱⁱ The area of niche construction, which involves the study of evolutionary dynamics in situations where populations modify their own environment (Odling-Smee, Laland, and Feldman 2003), although an interesting interface between ecology and evolution, poses a distinct set of challenges, and will not covered here.

^{iv} Ideas of population growth, which formed the basis for Darwin's theory of natural selection predate the theory of natural selection in Malthus' treatise on populations in 1798, and the mathematical formulation of the first model of regulated ("logistical") population growth, by Verhulst (Kingsland 1985, pp. 64-66).

^v I am referring to the Biometric and the Mendelian schools (Provine 2001); for examples, see the preface to Gause's book (Gause 1934), and Kingsland's analysis (Kingsland 1985).

^{vi} Efforts to fuse genetics and ecology were also made in the Russian school of ecology by people such as V.V. Stanchinskii (Kingsland 1985, pp. 150, 157-160; Mirzoyan 1996), the details of which I am unable to access.

^{vii} "Cultural differences" has been invoked as a reason for lack of communication between the two disciplines by proponents of the population genetics – population ecology synthesis. For example, Roughgarden (Roughgarden 1996) says, "The fusion of population genetics with population ecology can be compared to a prearranged marriage between partners who speak different languages. Although both families agree that the marriage is advantageous, it is somewhat difficult to achieve because of cultural differences."

^{viii} In Russia as well, there appears to have been developments of a similar nature (Shvarts 1977).

^{ix} In its objectives and methods, this field is now barely distinguishable from a recent off-shoot of ecology called “Molecular Ecology”, which originated in the 1990’s as a program to use molecular genetic methods to address problems in conservation biology, but then ceased to be a purely applied field, expanding and converging in its objectives and methods on Ecological Genetics. This is an interesting example of an inadvertent convergence of ecological and evolutionary fields driven by a common motivation.

^x The first model was actually developed much earlier, by Kostitzin in 1936 (op. cit. Christiansen 2004).

^{xi} Due to two main reasons: Adaptationism (a belief in the determinism of evolution) and theology (belief in a creator as the determining factor in biology).