



HUMAN EVOLUTIONARY DEMOGRAPHY

EDITED BY
OSKAR BURGER, RONALD LEE AND REBECCA SEAR



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2. Evolution in the History of Population Thought

Philip Kreager

This chapter places evolutionary demography in the history of population thought, and more particularly in relations between demography and evolutionary population biology. Darwin conceived evolution as a dynamics of variation arising from the behaviour of populations at intra- and inter-species levels. While Malthus's principle of population was an important early stimulus, Darwin resolved the core problem in evolution — how mechanisms of variation combine to produce divergence of character — by analogy to Smith's account of the division of labour. With the benefit of hindsight, we can describe Darwinian population thinking as the first general methodology in which it became possible to combine bottom-up observation, including enumeration of local population dynamics, with top-down statistical methods. The two components entail different concepts of population, which may be characterised broadly as “open” and “closed”. Their combination shows that evolutionary theory is rooted in the same sources of population thinking that gave rise to demography: the former lie in Classical population thinking and early modern population arithmetics, and the latter in nineteenth-century statistics and probability.

Hereditary influences remained a “black box” in Darwin's theory, which only began to be unpacked with the rediscovery of Mendel's research. The second half of the chapter traces the central role which demographic methods played in topical and analytical developments of the first half of the twentieth century, including both the formulation and critique of eugenics, the emergence of population ecology, and the rise of the mathematical theory of population genetics. There is an irony here: even as demographic methods came to play an integral role, mainstream demographers became less and less involved. The “separatism” of demography and evolutionary biology often remarked on in the post-war era thus has deeper roots. These lie partly in topical issues, like reactions against eugenics, but more importantly in a conceptual shift in how we understand relationships between ultimate and proximate mechanisms of population change, and its implications for analysis and modelling. Evolutionary theory entails a balance of methods and insights drawing on both population concepts, which demography has not yet achieved. The concluding section provides examples of how current evolutionary demography is now integrating these developments into demographic explanation.

By introducing population thinking, Darwin produced one of the most fundamental revolutions in biological thinking.

— Ernst Mayr

Demography is generally considered the pre-eminent social scientific study of human populations. Its methods and practices embrace all the social sciences and adjacent medical disciplines of population health. By a convention widely observed over the second half of the twentieth century, quantitative inquiry on human subjects in population biology (inclusive of genetics, ecology and other fields of evolutionary biology) has been viewed separately from demography, even though there is often significant methodological and substantive overlap. Of course, the latter fields also address other species, but often with a view to resolving problems faced by human populations. While the importance of genetic and ecological knowledge has in recent decades gradually come to be accepted by many demographers in addressing topics like mortality, ageing, resource sustainability and the implications of fertility declines, what may be called the “separatist” view has continued to prevail more widely. Going beyond contributions to the substantive topics just mentioned, however, there is a larger issue which may be called the knowledge impact of innovative science. Even slight familiarity with the discovery of DNA, of genomics and developmental biology is sufficient to recognise that the growth of population-based knowledge and applications in the several fields of evolutionary biology over the last half century has been nothing short of phenomenal. At present, whether we consider volume or funding of research, population biology arguably now constitutes the considerably larger domain of population inquiry.

There is thus a strong *prima facie* argument for demographers to reconsider the separatist view. After all, if concepts and models of population have proven so fruitful in the development of evolutionary research, the advisability of intellectual exchange is, at least, indicated. Yet so pervasive has been the separatist view that it prevails widely as a given or unstated assumption in demography, thus becoming an obstacle to rethinking relations between biological and social scientific domains. Mayr’s observation (1982: 487), above, is a case in point: that Darwinian population thinking *revolutionised* biology refers to developments quite unfamiliar in mainstream demography, and which might in consequence appear to carry no real importance for the discipline. History, however, shows otherwise. Darwin, in formulating the concept of natural selection, made population dynamics a central mechanism of evolution. To do this he relied heavily on population concepts foundational to population arithmetic and political economy in the seventeenth and eighteenth centuries that are also the sources of demography. There thus remains a common historical ground of population concepts, even though these fields have diverged subsequently.

The common ground is not of merely historical interest. The approach to population dynamics that Darwin initiated has remained truer to concepts and sources that first gave rise to quantitative research as a scientific approach to society. His population thinking achieved this by showing how core concepts of population prevailing before 1800 were fundamental to an evolutionary framework in which statistical methods were also key. As evolutionary biologists developed this combined approach in the late nineteenth and early twentieth century, demographic models and measures came to be seen as core components of population genetics and ecology; the greater explanatory power of this combined framework then underpinned the tremendous success witnessed in our era.

The purpose of this chapter is, first, to explicate Mayr's observation, and then to trace, going forward, the development of the concept of evolution as a locus of population thinking which has led to the recent revival of demographic interest in evolutionary research. The discussion proceeds in four steps. First, Darwin's population thinking is outlined. Here we follow its depiction in the influential "Evolutionary Synthesis" which Mayr, Dobzhansky and other evolutionary biologists put forward in the 1930s and 1940s, since their account remains the baseline from which contemporary population biology has grown. Second, Darwin's sources are reviewed, in order to establish the common conceptual ground of demography and evolutionary biology. This takes us back to eighteenth-century authors, notably Adam Smith, and to his early nineteenth-century followers (notably Robert Malthus), whose different concepts of population were brought together in Darwin's approach to concepts like variation and fitness. It is important to clarify how population thinking in demography and evolutionary biology are similar in major respects, but have differed in others. Two distinctions commonly employed in the literature (between open and closed population thinking, and between proximate and ultimate causes) are introduced for this purpose. It is striking that, although Darwin's own mathematics remained numerical, and the primary role of environment-organism interaction in his theory remained grounded in natural history, his recognition of the need for statistical inference in treating variation and fitness led to formal population models, like the life table, becoming a common ground of population genetics and ecology by the 1930s.

The third step considers developments in the late nineteenth and early twentieth century which took up the challenge Darwin's theory posed regarding how to integrate concepts and evidence from observational and field methods with concepts necessary for formal data collection and analysis. The Synthesis, which Mayr, Dobzhansky and their colleagues achieved, only occurred after several decades of controversy in which different ways of developing evolutionary population thinking were explored — with widely varying outcomes — in eugenics, public health, ecology and population genetics. The controversy over eugenics accounts in part for the hiatus that led demographers from the middle decades of the twentieth century to see their research separately from evolution. Yet there is a paradox: demographers turned away just as their methods were becoming core to mainstream population genetics and ecology. A more fundamental reason than aversion to the outlier of eugenics was the major factor in this turn; notably, whether a balance of open and closed population thinking was achieved. By way of conclusion, the final step in this story reviews problems related to scientific explanations that in recent decades have led demographers to contemplate their own methodological synthesis along evolutionary lines, and examples of promising research that are now emerging.

Population Thinking in the Emergence of Evolutionary Theory

Biologists' recent statements about the structure of evolutionary theory (e.g. Lewontin 2001; Gould 2002; Mayr 2004) emphasize relationships between three levels of population phenomena: genes (each individual's genome is a population composed of more than three billion DNA base pairs); organisms (each composed of populations of cells and organs that together form the several sub-populations, or demes, of which a species is composed); and environments (involving relationships within and between demic, and between species, populations, in the course of which environmental niches are occupied and constructed). As Darwin's theory gave a significant role to heredity, but was composed before the rise of genetics, these authors

take a historical approach that can be understood in three broad stages. The first begins with the logic of natural selection in the *Origin of Species* (1996 [1859]), noting unresolved issues that remained in Darwin's reasoning. The second then pursues subsequent developments: the rediscovery of Mendel's laws and ensuing controversies; the rise of population genetics; and the restatement of Darwin's programme provided by the Evolutionary Synthesis. The third then discusses the contemporary era of phenomenal growth in evolutionary biology opened up by the Synthesis, as well as limitations in the framework it has provided. This historical approach will be adopted in the inevitably much briefer summary given here.

Natural selection is a force or process in which variations that give an advantage to their bearers in the struggle for life are expected to accumulate in a species, and to have two major effects: firstly, they increase the adaptation of organisms to the environments in which they live; and secondly, they gradually modify the species. As Gould remarks, this process can be broken down into three components which provide the "syllogistic core" of Darwin's theory (2002: 125–41). *Variation* is arguably the most fundamental: the elemental fact that all organisms have unique characteristics requires not only that any species population is composed of a diversity of individuals, but that this population heterogeneity is continuously renewed. Natural historians before Darwin were, of course, familiar with individual uniqueness, recognising that such variation arises partly from adaptations to the environment, but also speculating that there must be a further internal process that guarantees the continuity of some traits characterising a species.

This second idea, *heredity*, was, until Darwin, normally accepted as consistent with Aristotle's founding natural history in which species are fixed, a view that resonated with later Christian teaching that all species were formed according to the original divine plan. Darwin sharply altered this picture, not only because his own extensive observation and compilation of evidence indicated that species are not fixed, but because he saw heredity as isotropic, i.e. a system that exhibits no preferred pathway of development. Hereditary sources of variation are, so to speak, the raw material of change, but impart no directionality. Copious small hereditary variations are observable in successive generations of offspring — i.e. much more variation occurs than is immediately advantageous in competition within or between species. In today's terminology, the additional variation is simply considered "neutral" — until, perhaps, environmental changes make a given trait a critical advantage or a liability. The key question, in any case, was how natural selection operates to promote certain hereditary variants, rather than others. Given the wealth of his own observations, and in the absence of a scientific account of the hereditary mechanisms now known as genetic mutation, recombination and drift, it is not surprising that Darwin's development of natural selection tended to focus on the decisive role of environment-organism relationships that vary across species and sub-species populations, rather than heredity.

The third syllogistic proposition of natural selection, *superfecundity*, further emphasized and reflected Darwin's primary concern to explain the force of variation. Referring directly to Malthus, Darwin observed that species tend to produce more offspring than can possibly survive (1996:54). Malthus's theory had postulated that, as over-supply would lead to competition for food between individuals making up a population, a positive check (i.e. mortality) would necessarily function to remove those members who were unable to compete successfully.

Gould brings these three propositions together in the following syllogism: (i) All organisms are characterised by internal (genetic) variation which is perpetually renewed in changing forms across generations; (ii) Only some offspring survive; (iii) Those organisms survive in which variation, by the action of environmental competition on inherited traits, yields traits enabling survival. Selection is a population dynamic in which species, and the sub-species groups that compose them, are formed and continually changed by the interaction of their members with each other, with other species populations, and with their environments. The deduction at the core of evolution is thus that selection is a creative force occurring naturally to favour the fittest organisms. As environments change, and individual and group actions proceed, and variations arise from this process, the characteristics of organisms and groups may diverge; this variation chiefly accounts for why a species is composed of several sub-populations with variant characteristics, but such divergence may also lead to the origin of new species.

In the course of later restatement of Darwin's programme, Mayr (1961; 1982: 67–72) introduced a simple formulation which helps to understand how this logic of divergence has shaped subsequent evolutionary thinking. His formulation remains widely employed although, as we shall see, it has come to be questioned in some respects that define current frontiers of research. Mayr contrasted the study of "proximate" causes of evolution to those concerned with "ultimate" causes. The former, addressed notably to characteristics of sub-populations within a species, has become the domain of molecular biologists (studying the recombination and transfer of genetic material) and physiologists (studying organic, cellular and sub-cellular mechanisms). Its role in explanation is to answer questions about how systems work, in which technical developments arising from laboratory methods and mathematical modelling since Darwin's time are pre-eminent. Of course, natural historical studies of individual and species adaptation in varying environments have long been concerned with proximate causes. Ultimate causes address why history in the long term has, for a given species, produced one system of adaptations rather than another. Research, for example in systematics (i.e. the natural history and classification of systems of speciation) and paleontology, retain a strong focus on Darwin's concern with variation arising from organism-environment interaction, in which causes are the product of the lived conditions of many thousands of generations of natural selection. Put another way, proximate causes are the immediate factors that determine the selection of genetic materials that occur in an individual and their physiological correlates; ultimate causes are conditions responsible for the evolution of genetic traits and correlates with which every individual of a species is endowed.

Variation and the Problem of the Renewal of Population Heterogeneity

If Darwin's reliance on Malthus is all there was to his population thinking, then evolutionary approaches would have little to add to demography. Indeed, Malthus's theory on its own would not have enabled population thinking in evolutionary biology to achieve its remarkable advances in explaining how and why the characteristics of individuals, and thence sub-populations, diverge. Superfecundity and the positive check remain, of course, key to the general logic of what limits population size and growth, but they are parameters that set only the outer limits towards which population increase in any species or sub-species may tend. The positive check is not in itself a mechanism of agency, only of restraint. It comes into play where environment-organism interactions reduce numbers by eliminating individuals and, ultimately, groups.

The idea of the positive check nonetheless contributed some important dynamic components to Darwin's population thinking, notably as a mechanism of stabilisation, and it also contributed to the centrality of intra- and inter-species competition as an ultimate cause underlying natural selection. The operation of proximate mechanisms, however, remained primary, since environment-organism interaction was crucial both to arbitrating hereditary sources of variation and to when and where the positive check might operate. In other words, evolution as a process of population change is not simply about mortality or fertility, i.e. *population renewal*. To understand how species evolve we need to identify mechanisms that ensure the *renewal of population heterogeneity*, i.e. what enables the continuing flow of new characteristics which can be transformed into adaptive advantages, thence leading to further adjustments in population memberships, composition, size and structure. The syllogistic core of evolution thus gives an incomplete account of a critical element in population thinking that concerned Darwin: how population variation functions as a *creative force* in evolution.

It will help, to begin with, to clarify how Darwin goes beyond Malthus. We can then turn to a key source of the "revolution" he initiated, which drew on a much older model of population thinking that prevailed in the era before the nineteenth-century rise of statistics and demography. More particularly, Darwin relied on analogies to Adam Smith's powerful restatement of the Classical model of population, in which the specialisation and interdependence of individuals — and the sub-populations to which they belong — in the division of labour provide the primary motor of social, economic and population change. Comparison of the two different conceptual approaches of Smith and Malthus as they shaped Darwin's population thinking allows the distinction between two fundamental modes of population thought — open and closed — to be introduced descriptively. We see, firstly, how Darwin brought them together tentatively as complementary components of evolutionary theory; and secondly, the tensions that nonetheless exist between them.¹ Section 3 then turns to the struggle to reconcile these tensions as Darwin's framework was developed in the later nineteenth and early twentieth century.

Darwin's "Malthusian Episode"

Malthus (1982 [1798]) considered that any population is constrained, sooner or later, by the limited carrying capacity of agricultural production in a given terrain. A population, in other words, exists in a fundamentally *closed* environment, and can only expand up to the limits of its productivity. Behaviour leading to population growth in excess of productive capacities, and a consequent and widespread positive check, is immoral, especially as it affects infants and children. He therefore argued that only one demographic response is legitimate: the regulation of fertility via the preventive check, i.e. the delay or foregoing of marriage so that fertility is restrained to levels at or below what agricultural production can support. As Wrigley (1986) has shown, Malthus conceived the operation of the positive and preventive checks as a system of feedbacks: a population as it grows may for a time expand production, but it will inevitably reach the limits of such adaptation, and the humane adaptive response of the preventive check is then necessary. Historical demography, and more recent population history, have shown, of course, that much more than nuptiality control is involved and many other factors may be

1 For historical background to the Classical Model and its subsequent development in population arithmetic, political economy and population renewal theory see Kreager 2008, 2009 and 2017.

important. As Wrigley also notes, Malthus was wrong about the natural limits of agricultural productivity, which was not a closed system, even in his own era (1986: 50–53). Yet the idea that the timing and extent of marriage function as feedback mechanisms that may serve to adjust mortality, fertility and population growth relative to the surrounding environment, has proven apt in some periods of European history, and conceptually fruitful.

Adopting Mayr's distinction, we can see that Malthus aspired to formulate a theory of ultimate causes. His admiration for Newton's law of universal gravitation as a model of explanation is well known (e.g. Flew 1982: 32). While aware, for example, that societies have diverse family, marriage and productive arrangements, and that the positive check may operate to a differing degree in them, Malthus considered such variation a secondary matter, i.e. such factors might delay, but could not fundamentally alter, the ultimate impact of superfecundity, the necessity of the positive check, or the single solution of nuptiality control. The principle of population put forward in his *Essay* thus propounds an absolute, closed and concise model of limits to population to which all must in the end conform.

Such a dismissal of the central importance of variation was obviously of no help to Darwin. Indeed, if the positive check, as the sole and ultimate mechanism of selection, continually removed less successful individuals — with no account being given of how variation renews population heterogeneity — then the long-term evolution of populations would see only the progressive reduction of sources of variation, leaving populations composed of increasingly perfectly fit members in each species. In Darwin's view, however, the diversity of environmental adaptations, together with the isotropy of heredity, guaranteed that natural selection has no such foresight or drive to perfection. Indeed, the reduction of heterogeneity effected by the positive check on its own would have the opposite, disadvantageous, effect by leaving populations vulnerable to circumstances in which environments change.

Darwin's evidence, in any case, showed the contrary: environment-organism adaptation rested on the specialisation of individuals to suit the environment, and as individuals faced competition and colonised new niches, then new specialisations and sub-populations characterised by them were found to emerge. Changing symbiosis with other species also occurred in this process, enabling ever denser development and habitation of a given setting. In this process, population heterogeneity was continually renewed, and this became possible because sub-populations making up a species are not actually closed, but *open* — i.e. they have mating, migratory, and other relations with species members. Both intra-species variation (whether arising, e.g. from mating within a given deme or species sub-population, or between them), and changing competition between species, are entailed. Population heterogeneity and openness are thus jointly critical mechanisms of evolution.

Historians of biology have found that Darwin left notebooks, letters and marginal comments in texts he had read which enable them to trace the development of his population thinking in considerable detail. Schweber (1977: 231–32, 286–96) provides a detailed account of Darwin's "Malthusian episode", and of his subsequent development of biologists' reading of Adam Smith, which gave form to his account of heterogeneity and openness. The Malthusian episode came early in the conceptual development of Darwin's theory (in 1838). At that time, he, like Malthus before him, was strongly disposed to the theoretical ideal in which laws define ultimate determinants. When quantitatively formulated, such laws reveal central tendencies that ensure the stability of natural systems while allowing for many surrounding random

and other fluctuations. He was greatly interested in this form of theory, and not only because the pre-eminence of mathematically defined physical laws was accepted as canonical in the intellectual milieu in which he lived. Of more immediate concern to Darwin was the complexity of his natural historical evidence, which led to the view that, amidst the copious variation that heredity made possible, the process of evolution via environment-organism interaction worked to produce only small and gradual changes within demes and species, normally over long periods of time. This gradualism, together with the uncertainty of the exact nature of the hereditary component (which he assumed to act randomly), led him to the view that divergence of character could only be established with the help of a statistical conceptualisation of change. In other words, the creative agency of environment-organism interactions acting on the flow of hereditary variation should be expressed in terms of predominant frequencies amongst a vast array of different outcomes. In this way it might be possible for biological theory to emulate the general law-like mathematical formulation of the physical sciences.

More particularly, Darwin's interest in Malthus was kindled by accounts of the latter's theory given in Quetelet's (1869 [1835]) social physics, and in contemporary reviews that discussed Quetelet in relation to Malthus, which Darwin studied closely. Quetelet, arguably the foremost European exponent of a new science of population statistics, drew on his experience as an astronomer to propose the idea of "*l'homme moyen*", or the statistical normality of the "average man". Linking this to Malthus's account of superfecundity and the positive check appeared to open up the possibility of formulating deterministic or ultimate laws of society analogous to those of physics. The often-cited passage in Darwin's *Autobiography* (1958: 120), where he remarked on the epiphany that the *Essay on Population* represented in the development of his theory, directly follows the 1838 notebook passages in which he considered Quetelet (Schweber 1977: 293). In short, what Darwin derived from Malthus was not only the ultimate constraint of the positive check. This constraint provides an ultimate causal mechanism for evolution in so far as the will to survive or avoid death becomes the premise on which competition for existence rests. More than this, Malthus's theory appeared as an exemplar of the whole view of scientific theory in which quantitative systems are governed by deterministic laws that allow variation within long-term tendencies to stabilisation.

As Darwin quickly recognised, however, Malthus's checks and Quetelet's statistics of normal tendencies unfortunately left out the critical explicandum of the proximate mechanisms of variation.² There is, put very simply, much more going on in the lives of species members, or individuals and groups in society, than competition for survival and the average outcomes of such a process. Not everything that heredity and environment-organism interaction generates is telling for the divergence of demes and species, and even if significant for divergence the effects may only become important later in history. Darwin therefore turned his attention concertedly to the problem of how to formulate a cohesive theory of the creative process of variation.

The logic of the division of labour, which already existed as a model embracing population heterogeneity and openness, and had been remarked by natural historians (Kreager 2015: 76–77), became the focus of his attention. His familiarity with this logic as applied to biological processes emerged by the 1840s in his detailed notes on Milne-Edwards' *Introduction à la zoologie générale* (1851 [1834]), and other writings to which he had access (Limoges 1968,

2 Schweber notes that the review of Quetelet's book which Darwin annotated concluded with remarks on this inadequacy (1977: 293).

1970; Schweber 1980: 249–57). Milne-Edwards worked in an established natural historical approach known as “animal economy”, and employed the phrase “division of labour” to explain how organs in the body become progressively specialised. His development of this analogy closely followed the line of reasoning in Smith’s *Wealth of Nations* (1976 [1776]). Just as Smith describes how society and economy evolve from hunter-gatherer groups in which all individuals carry out the same productive, military and other functions, Milne-Edwards describes how, in simple organisms like polyps, bodily functions are not differentiated; just as agricultural and commercial societies advance beyond the simplest level of social organisation by developing specialised personnel for agriculture, defence, manufactures, transport and so forth, so species become more complex by developing specialised organs for respiration, digestion and reproduction (cf. Milne-Edwards 1827 and Limoges 1968 to Smith 1976 vol. I: 689 et seq. and Kreager 2017).

Darwin, like Smith, readily came to view the idea of the division of labour as of major importance at the population level. Both authors considered the renewal of the many and heterogeneous groups, and the emergence of new populations with specialisations productive in changing environments, as key motors of historical and evolutionary change. Darwin’s elaborate development of the analogy between the creative force of variation and the division of labour in human society is extensive and detailed, and a few examples will have to suffice here to give the reader an idea.³

Transferred to the population level, Milne-Edwards’ account of the development of specialised organic characteristics becomes an account not only of physiological development in individual members of a group, but of how such greater or lesser divergence characterising species sub-populations translates into their greater or lesser adaptive capacities for expanding into environments available to them, and the heterogeneity of groups that comes to characterise such sites. As these capacities become manifest, accompanying changes in population composition, size and growth follow suit. Darwin, citing Milne-Edwards (1996: 92–98), illustrates his argument by many examples drawn from competition amongst *flora* and *fauna*, leading to his famous diagram of species divergence.⁴ Such specialisation, as in Adam Smith’s

3 Comparison of Darwin’s and Smith’s population thinking draws on Schweber (1977, 1980) and Kreager (2017). Schweber further remarks on the status of the division of labour as a widely employed metaphor and model in the mid-nineteenth century. That said, Darwin’s debt to Smith’s account of population specialisation, interdependence and the renewal of heterogeneity as fundamental elements of the dynamics of evolution should not be overstated. As with his incorporation of Malthus’s positive check, Darwin sought analogies that would enable him to think cohesively about observed processes recorded by natural historians — *not* a systematic reduction of biological phenomena to principles supposed to regulate political economy. This is evident merely in the fact that most types of feedback in environment-organism interaction differ from those in the division of labour, and Darwin did not pursue analogies to Smith’s population thinking further than its general logic. As we shall see, in providing a place for formal, statistical analysis of variation in his theory, Darwin’s logic marked a major advance on Smith, which is central to the “revolution” remarked by Mayr.

4 Thus, “In an extremely small area, especially if freely open to immigration, and where the contest between individual and individual must be severe, we always find great diversity in its inhabitants. For instance, I found that a piece of turf, three feet by four in size, which had been exposed for many years to exactly the same conditions, supported twenty species of plants, and these belonged to eighteen genera and to eight orders, which shows how much these plants differed from each other. So it is with plants and insects on small and uniform islets; and so in small ponds of fresh water. Farmers find that they can raise most food by a rotation of plants belonging to the most different orders: nature follows what may be called simultaneous rotation.” (1996: 94).

account of the division of labour, is closely bound up with the interaction or interdependence of sub-populations in a given productive environment. For Smith, the specialisation of tasks in the division of labour both develops individual capacities and characteristics, and requires many productive groups to work in close interdependence; expanded capacities for individual agency and production enhance general living conditions for the several sub-populations involved in a given productive niche, affording them competitive collective advantages in their wider environment; this entails not only enhanced economic but social agency. Specialisation and interdependence of constituent populations making up a society are thus a principal motor of their own and general social change, and the integral role of population composition, size and growth in the evolution of economy and society is explained by Smith in these terms. In essence: “the number of workmen in every branch of business generally increases with the division of labour in that branch or, rather, it is the increase of their number which enables them to class and subdivide themselves in this manner” (1976 vol. II, Introduction, p. 277). Population, in other words, tends to increase in sub-populations working in tandem in a given economic sector or sectors, and this becomes a motor of population growth in society more generally. By analogy, Darwin “chose the principle of optimisation of the amount of life per unit area as the overall explanatory principle” (Schweber 1980: 288).

Thus, both Smith and Darwin considered (contra Malthus) that the growth of a population was not only key evidence of its competitive success, but that such growth was itself a principal mechanism of improvement. Competition at the individual level may ultimately be decisive, but is conditioned by the structure of interdependence between populations, which conditions the circumstances in which an individual acts. Darwin therefore, like Smith, considered the positive check as functioning in *proximate* terms, that is, as conditional on environment-organism interactions and on the nature of relationships within and between *local* populations — rather than, as in Malthus, an *ultimate* or universal mechanism to which all populations and all members must sooner or later answer in a particular way. Rather than fundamentally and ultimately closed, population dynamics are by nature open, as groups exist in manifold relationships and interdependencies with other groups. These interdependencies, as in Smith’s analysis, give Darwin’s account a much more extensive set of organism-environment feedbacks than Malthus’s singular stress on the positive and preventive checks in an ultimately closed environment. As Schweber remarks, Darwin’s whole approach reflects a critical difference between Smith’s account and Malthus’s: individual species members have much more agency in dealing with proximate causes than is possible under Malthus’s emphasis on the ultimate necessity of his two checks on population (1977: 283; Kreager 2017: 531).

This emphasis on the agency that diverse group members exercise in producing variations followed directly from the much more extensive body of direct observation of adaptive processes that characterised Darwin’s natural history, in contrast to Malthus’s political economy. For Darwin, explaining processes of population change rests first on empirical identification of proximate causes, as these arbitrate the possible operation of ultimate positive checks. Put another way, the inter-relationships between groups in a given environment requires a bottom-up perspective: explaining population dynamics begins in observation at lower levels of aggregation, since changing group compositions and interrelationships carry implications for higher levels of aggregation, both in the short and long term.

Two Concepts of Population

Darwin's quantitative skills remained those of a botanical arithmetician, employing methods similar to those of seventeenth- and eighteenth-century population arithmetic; his notebooks make clear that he was not adept at higher mathematics.⁵ Yet, as we have seen, his population thinking was prescient in understanding that the different conceptual approaches to population underlying Smith's and Malthus's works are both necessary to explaining how populations evolve. From the former Darwin took the idea that populations are by nature open and heterogeneous, variation arising in them from the interdependence of groups and their members, which he saw as analogous to the way specialisation functions in the division of labour. Such open population thinking was a breakthrough in showing how the vast body of his natural historical evidence could be generalised at the population level.⁶ It did not, however, satisfy the scientific criteria expected of theory in the milieu in which he wrote. As remarked earlier, the middle decades of the nineteenth century were an era in which the rise of population statistics led to its proposed formalisation as a social physics (Porter 1986).

Lacking close familiarity with the new methods, Darwin nonetheless responded to this second idea of population by drawing on contemporary views of Malthus's *Essay*, in which the impact of the positive check was understood as imposing absolute limits on population suitable to developing methods of social physics. The mortality of the positive check could be used to define limits to growth for any population given the particular environment in which it is found. Darwin hoped such an approach would enable statistics to demonstrate changes in the frequencies of specific evolutionary traits.

As we shall see, this proposition proved very difficult for Darwin's followers to develop in the late nineteenth and early twentieth century. Before turning to their several formulations — some brilliant and of enduring importance, whilst others have come to be recognised as not only dubious but dangerous — we can at least try to state succinctly the fundamental problem posed by Darwin's dual approach to population: his open population thinking, grounded in natural history and the role of environmental constraints in shaping evolution, is analytically distinct from, and may even seem opposed to the closed populations on which formal modelling depends. The extent to which Darwin was himself aware of this difference remains uncertain. It was brought out at least as early as the 1920s by the doyen of twentieth-century formal demography, Alfred Lotka, whose mathematics of population ecology (1925) was one of the earliest evolutionary formalisms to be established, and then extended to human fertility and mortality (1934; 1939). What Darwin appears to have been the first to recognise, at least implicitly, is that the two concepts, even if radically different, are nonetheless complementary. How, then, did he bring open and closed population thinking together? What problems then remained, that generated such variously seminal and flawed approaches amongst his followers?

5 For example, in making an estimate of relative frequency, Darwin made multiple calculations each based on different ways of proportioning a population, and then compared the results — in effect, reinventing a method Graunt had devised two centuries earlier (cf. Browne 1980; Kreager 1982).

6 Darwin adopted Classical population thinking not only because it was a model that was integral to Smith's account of the division of labour and early quantification of human society, but because it was also established practice in natural history. Thus, in his extensive comparative study of barnacles (1851), he drew on the large body of data available in natural historians' plant catalogues, and the established field of botanical arithmetic, in which counting and comparing physical characteristics was a standard practice (Browne 1980).

The closed character of formal population analysis and data systems needs, of course, no introduction to a twenty-first-century audience of demographers and population geneticists. Lotka used his training in physical chemistry to argue the generality of this scientific methodology.⁷ Whether in thermodynamics, census-taking, life table construction or the theory of population renewal which was Lotka's own contribution — the individuals making up a population are treated as identical subject to the system of classification employed. Just as the behaviour of atoms and molecules conforms to the rules of the periodic table, so the population movements of human beings conform to the fixed set of statuses given, for example, in a census schedule. Censuses, like the periodic table, have the considerable advantage of being effectively comprehensive, thus enabling exhaustive and purely formal analysis of all changes of state between recognised categories. Once born, an individual can only move between classificatory statuses: he or she gets older, marries, establishes a household, has children, changes occupations [...] and eventually dies. Closed units, whether of the total population under analysis, or of any of its component sub-populations, enable aggregate states of population change to be calculated precisely: age and sex structures, gene frequencies, life expectation, trends in fertility, mortality, labour force participation and so forth. This approach, which Mayr and other contributors to Evolutionary Synthesis referred to as “typological” or “essentialist” (1982: 47), is immensely powerful once species and demic populations have been identified.

Darwin's *Origin* was, however, concerned not only with the renewal of existing populations but *the renewal of population heterogeneity*, since evolution proceeds by continuing adaptation and consequent variation in and between populations. To begin by treating populations in nature as closed is artificial. As natural historians had long recognised, species rarely present themselves as discrete groups in nature. Sustained observation is a first necessary step, to identify the role of environmental factors in shaping variation at local levels. Such open inquiry decides which characteristics should be tracked, and in which environments. Identifying the relationships between individuals that appear to constitute membership of a species involves repeated hypotheses and continuing observation to test them, until the unity of a proposed species can be considered established. Of course, the rise of genetics since Darwin's time has provided further laboratory methods of observation that greatly assist identification. Nonetheless, the primary questions necessary to track variation and possible divergence remain: “What is a population (i.e. for the purpose of differentiating organisms in the process of variation)?”; “What set of sub-population units comprise a species?”; and “What relationships account for their differences?”

Natural historians up until the late nineteenth century employed enumeration as part of open population thinking, i.e. accepting that an exhaustive or complete counting was only exceptionally realisable. Similar to Graunt and other early modern population arithmeticians, totals could be compared without formal mathematics and without comprehensive census inventories. Where characteristics appeared to clearly differentiate groups, they were accepted

7 Lotka sets out the analogy between species populations and those of molecules carefully and elaborately, emphasizing that his analysis is confined to “isolated systems” (1925: 26) and that, as in all probabilistic models, possible events and relations are limited to those specified by classifications in advance (1925: 35; 41). When he later came to develop the model for human fertility and mortality, he was able to say more simply that analysis by definition is confined to “closed populations” (1939:11). The following very brief summary can scarcely do justice to his extended presentation.

as indicating the presence of distinct phenomena whether the entity was a plant or animal in the wild, a human being recorded as dying of a specific disease in the “mortality bills” that were the only record of causes of death before the modern census era. Darwin, in effect, moved on from his predecessors by the simple step of accepting that a carefully observed body of numerical evidence at the population level — however provisional — was effectively complete. This appeared to be a substantial improvement on previous practice that was not population-based, in which whole species and higher types might be proposed from merely a few specimens.

Darwin’s reasoning, as we have seen, addressed variation and the divergence of species in terms of optimisation: the amount of life that could be supported in any setting would become greater, more diverse and complex as competition intensified; larger genera, species and demes would tend to produce more hereditary variation, in which those offspring with more diverse characteristics would have additional advantages to adapt and increase their numbers. Such a local “division of labour” in this way provided a plausible account of how particular adaptive advantages could accumulate at higher levels of aggregation, further encouraging Darwin to think at the level of populations. As Schweber remarks (1980: 288), Darwin’s premise that the quantity of life is gradually optimised in local environments effectively bypassed the difficulties of integrating different levels of description: local observation of open populations, in which characteristics are gradually differentiated as inquiry proceeds, seems to flow seamlessly into later analysis in which units of population might be defined formally as distinctive demic and species populations, i.e. treated as closed for purposes of statistical analysis. Indeed, as an empirical procedure for generating and testing hypotheses, this logic appears straightforward. Hence Darwin could hope that emerging emerging statistical techniques could be applied to variation and divergence, even if his own understanding did not extend to how formal models and data systems are actually constructed.

What this way of thinking assumes, however, is that the role of open population thinking — sustained local observation of proximate relationships in order to differentiate units of population — has been carried out prior to statistical modelling. With the benefit of hindsight, we can see that, for a scientist of long natural historical experience like Darwin, this “bottom up” approach was so elemental it could not ever be questioned. Formal analysis, however, can take place whether or not sustained observation has given an empirical ground to hypotheses, and whether or not local processes are translated accurately into specifications of closed population units entailed in large datasets. We turn now to subsequent developments in evolutionary theory, which proved to be fraught with controversy. Apparently powerful arguments claiming to establish ultimate causes were built on the basis of classifications and units of measurement not grounded in observation of proximate causes. Arguably, one of the critical lessons from the emergence of evolution as a population theory is that confusion and ambiguity proliferate where the different roles of the two concepts of population, and their engagement at different stages of analysis, are not recognised.

The Early Struggle to Incorporate Population Genetics and Demography into Evolution

In this short account, we will consider two contrasting approaches of the late nineteenth and early twentieth centuries which illustrate this issue: Galton’s attempt to use evolution to build a science of eugenics; and the several contemporaneous movements in early-twentieth-century

population thinking that led to the consolidation of demography as a discipline, and gave its methods a fundamental role in population genetics as a core component of the Evolutionary Synthesis. This period stands as something of a paradox for demography: as the discipline gradually took its contemporary shape, its formal methodologies made significant contributions to population ecology, to the critique of eugenics and to the formulation of the Synthesis — yet its professional stance became increasingly separate from evolutionary biology.

Galtonian Eugenics

Darwin's need to treat heredity as a "black box" in his theory led to an immense amount of speculation and exploratory research (Provine 1971). As Porter (1986:280) remarks, Darwin's own later ruminations on this problem were "virtually a complete failure amongst biologists", although they attracted the attention of the biometric school developed from the 1870s by Galton and Pearson. Both men were remarkable polymaths whose life work focussed on developing advanced statistical techniques to track the evolution of hereditary and racial differences, which they then put forward to legitimise highly controversial public policies. Darwin had speculated that hereditary took the form of particles or "gemmules" that circulate in all parts of the body, transmitting specific traits particularly in the course of embryo formation (1868). He was led to this in part by questions concerning the role of evolution in shaping human society. Galton, for whom the latter concern was paramount, redeveloped the gemmule hypothesis not as a matter of embryology, but as a demographic phenomenon. For this purpose, he prioritised the Malthusian component of Darwin's theory — superfecundity — as the primary force in evolution. Reproduction, Galton argued, arbitrates the role of heredity in human and social development, since varying levels of fertility within and between groups in a population determine which, and how widely, certain hereditary characteristics rather than others come to predominate; fertility differentials constitute "reproductive selection", the importance of which is vastly greater as a factor in natural selection than environment-organism interaction. He coined the term "eugenics" to refer to an ostensibly scientific and statistical practice that would ensure that only the best babies could be born. Not only should those judged the most fit members of a society be encouraged to reproduce, steps should be taken actively to restrict the fertility of less desirable groups. As Galton repeatedly emphasized, the majority of offspring were being produced by only certain (lower-class) groups in society. Eugenics rapidly became highly topical in an era in which European reproductive levels had for the first time begun to decline radically.

To understand the impact of reproductive differentials on the quality of human populations, Galton needed a statistical method that could discriminate between more and less powerful influences on genetic transmission. This led to his famous conceptualisation of statistical correlation and regression, and their formal mathematical development by his associate, Karl Pearson. Both concepts, of course, have come subsequently to play a widespread role in population research. Their use in eugenic argument, however, relied on institutional and popular definitions of social class differences, ascribing ultimate causes to them without examination of their empirical basis.

While insisting on their allegiance to Darwin's and Malthus's theories, Galton and Pearson argued that there were crucial flaws in their reasoning. Darwin, as noted above, did not give sufficient attention to reproductive selection. Malthus did not go far enough in his criticism of a supposed lack of sexual restraint among the poorer classes; while recognising that their superfecundity leads necessarily to the action of the positive check, he did not ask whether that

check would actually be sufficient, i.e. whether there would still be a great majority of lower-class children relative to those of higher classes. The normal function of mortality Galton and Pearson termed “the selective death rate”, i.e. the ultimate mechanism of natural selection in weeding out the less fit. Average family size had, nonetheless, remained higher in lower-class “degenerate and pathological stocks” (Pearson 1912: 27). Hence the dire prospect, if the positive check did not remove the greater majority of lower-class children, of their superfecundity of surviving children to greatly outnumber those of “the cultured and highly sensitive upper and middle classes”; the outcome would be “race suicide” which, “in the inmost recesses of history [...] explains the fall of great world-civilisations” (Pearson 1912: 10, 39).

The central issue, for eugenic argument, was thus how to demonstrate this calculus. Correlation, Galton remarked, provided the method demonstrating “the closeness of the relation between any two systems whose variations are due partly to causes common to both, and partly to causes special to each” (1907: 174). Pearson’s mathematical development, appearing in his note on reproductive selection to the Royal Statistical Society (1896), begins with statistical demonstration of the correlation between fertility and organic characteristics across generations. For this purpose, he employed a classic measure in social physics — height — in this case of mothers, daughters and wives in “1,842 families of Danish race”. Pearson showed a regular percentage change in height across generations; he would later describe such variation as an instance of “the law of ancestral heredity”, i.e. the change of any organ or physical or mental characteristic that typifies its spread in a large population over time (e.g. Pearson 1912). The question, then, was what part of the Danish population was contributing most to such changes. Analysing net fertility (i.e. allowing for infant and child mortality, and for non-marriage) in artisan and professional classes, Pearson concluded that while the former represented only 27 per cent of the population, its greater fertility produced over half of the younger generation. In short, on this account reproductive selection is the much greater factor than natural selection (i.e. as defined only in terms of the selective death rate) in population replacement and change.

Pearson’s “The Problem of Practical Eugenics” (1912), is one of many articles in which he developed this mathematics of correlation as a basis of demographic policy, particularly in the context of the fertility declines now commonly known as demographic transition. Anticipating later demographic interests, he was particularly concerned with the economic value of children, notably the impact of factory legislation which had removed the value of child labour as a component of working-class family incomes. His analysis assumes the “law of ancestral heredity”, and is directed particularly to showing that well-intentioned government policies supposed to improve the environmental conditions of factory populations are much less important to national development than their impacts on heredity. He traces fertility declines in the Registrar General’s data for a number of manufacturing towns and rural areas, particularly in the period 1870–1905, in relation to the several Acts that prohibited child labour. He notes not only the steep decline in birth rates, coupled with the still relatively larger family sizes of the working classes, but levels of tuberculosis, insanity, deafness and other conditions he considers pathological, calling attention to their incidence by birth order. As these conditions are markedly more common in the first, second or third child a woman bears, Pearson concludes that not only are working classes producing a higher percentage of the population, their reproduction ensures a higher percentage of “cacogenic” stock overall. Meanwhile, the upper and middle classes have come to have an “artificial birth rate” in consequence of their inclination to lower fertility in the

context of changing economic conditions. Pearson then traces the implications of these several developments in relation to demographic topics that have proven of long-term interest, notably contraception and ageing. More immediately, Pearson advocated major changes to taxation, (raising rates on income, estate and inheritance for the childless); while factory legislation should not simply be repealed, its continuing impact on the “racial efficiency” of the population could only be countered by amplifying the numbers of “well-born children”.

Both Galton and Pearson played major and respected roles in scientific organisations of the time, and both were offered knighthoods.⁸ Their eugenics is a reminder that distinguished authors claiming to be followers of Malthus and Darwin may, in fact, be promoting theories that are hardly consistent with such claims (cf. Kreager 2014). On the statistical side of population thinking, there can be no doubt that their work constituted a serious and imaginative attempt to address fundamental problems of conceptualising and measuring structural changes in frequencies across generations, of the logic of population stabilisation given incomplete genetic data, and of the incremental or “small steps” by which genetic variation influences population change. Their technical insights, however, were vitiated by two radical departures from the evolutionary structure of population thinking that Darwin had carefully developed: their predilection for arguments based exclusively on ultimate causes; and their sole reliance on closed or typological population thinking.

In eugenics, heredity displaced Darwin’s emphasis on environment-organism interaction in the study of variation. Pearson considered heredity “more potent”, adding acerbically that population policy makers should know that a stud productive of Derby winners does not rely chiefly on improved stables (Pearson 1912: 36, 38). Eugenicists’ pursuit of heredity as the seat of ultimate causes was, moreover, built upon incomplete and ambiguous definitions of the human sub-populations treated in published statistics, and the more or less complete exclusion of sub-population interactions that, as proximate causes, were crucial to Darwin’s view of evolution. The populations Pearson employed were drawn from standard institutional sources in which classification rested on criteria not informed by observation of how groups are formed, sustained and related over time. Given Pearson’s “cacogenic” arguments, it is also evident that the classifications selected were in consequence all the more susceptible to powerful class and other biases. Pearson in effect extended closed population thinking to human heredity in ways that run counter to Darwin and Mendel: all genetic and physiological characteristics other than those mentioned above were taken to be identical for all individuals in each given population type; all genealogical or other links that show members’ involvement with other populations were not considered; and change over time was always directed, i.e. not isotropic.⁹ In the end, the eugenic exercise excluded a vast array of sources of variation, and was strongly tautological: those groups with higher birth and death rates were categorised from the start in closed classifications as “cacogenic” or “degenerate”.

8 Pearson refused, being a socialist.

9 Pearson admitted in a footnote (1896: 398–39, n.4) that his statistical approach via correlation puts aside Darwin’s central concern in the *Origin* with how variation can give rise to new demes and species. Pearson reduces fitness to progressive change in extant species defined as composed of homogeneous social classes.

Vital Statistics, Population Ecology and Genetics: Some First Steps toward an Evolutionary Demography

As we have seen, Darwin's conviction that statistical evidence is essential to understanding evolution as a process of population interaction embraced both numerical observation at the local level and the potential for modelling aggregate frequencies at higher levels of analysis. In evolutionary biology, the famous breakthrough that swept away eugenic and many other arguments came at the local level: the rediscovery in 1900 of Mendel's experiments on genetic variation in peas. Mendel's work differed sharply from the eugenicists in the careful observational method used to establish sub-populations and the nature and structure of their relationships.¹⁰

With the benefit of hindsight, the early biometricians' eugenic project may be said to have occupied a kind of median position between the continuing research of evolutionary biologists and the much wider period concerns about the potential impact of declining birth and mortality rates, race, and migration on national population composition and replacement. Controversy over the role of reproductive selection embraced vital statistics, public health, biological anthropology, sociology and a great many essays (variously of socialist, conservative, feminist and other persuasions) written for general audiences (Soloway 1982). The issue was one of general public concern. Eugenics, with its technical claims and dramatic highlighting of demographic differentials as simultaneously social and genetic determinants, attracted widespread attention, and was without doubt a major stimulus both to controversy and to recognition of the need for more critical, observation-based approaches. Developments in social and vital statistics were, of course, for the most part of a fundamentally different kind from Mendel's work, since they relied on closed-population datasets established during the nineteenth century with the founding of national statistical offices and professional statistical societies, and the dream of a social physics.

These data provided the foundation for several environmental reforms, including those Pearson attacked, and for declines in mortality related to these reforms at all but the youngest age over the later nineteenth century. They also, as we have seen, provided primary evidence of fertility declines. Vital and social statisticians thus felt a strong need to respond to the eugenicists' arguments, but they also faced uncertainty regarding the specific mechanisms underlying differentials in fertility and mortality between social groups. Their response was to tighten and extend the actuarial approach on which demography rests. This response was

10 Although outside the immediate topic of this chapter, Mendel's method independently encapsulated the combined open and closed population reasoning that Darwin pioneered. Peas of seven seed types were selected, merely on the basis of visible distinctive characteristics (smooth, wrinkled, white, etc.). This selection amounts, in effect, to a pragmatic hypothesis that such features indicate genetic variants. The seven types were planted, and numbers of offspring consistent or variant with the original types noted in the outcomes for each planting. Self- and cross-fertilisation of offspring were then carried out in regular combinations across a succession of generations, and the outcomes enumerated. In this genetic demography of peas, the question 'What constitutes a population or sub-population?' is left open, and the specification of the several sub-populations emerges as a key result from observation, including the ratios that give the regular proportions of dominant and recessive forms that arise from the relationships between them. In effect, the behaviour exhibited in the experiments sorts the population into recurring groups defined by their observed qualitative and quantitative properties (of which the most famous is Mendel's is 3:1 ratio expressing the incidence of dominant versus recessive traits); such regularities then become properties that can be tracked and modelled in wider surveys and in other populations.

characteristic of three major innovations in which demographic methods became fundamental to addressing problems in population biology in the early decades of the twentieth century. The first emerged in part as a response to eugenics, while the second two were driven by problems in evolutionary biology.

The first development, reflecting concerns over differentials in declining fertility, led the General Registry Office (GRO) in England and Wales to put the need for a comprehensive social classification scheme on its agenda. As Szreter's (1986) study of the GRO's programme has shown, its class schema was designed to refute eugenic arguments, although the alternative mechanism put forward to explain fertility declines (the rise of contraception) remained inadequately documented. In addition, a detailed family census was conducted, in 1911, which included more variables, such as parity, than existing censuses. As Szreter (1986: 538–40) remarks, the GRO social class scheme, which remained largely unchanged until the 1970s, continued to reflect several problematic eugenic assumptions which reduced the forms of variation that could be tracked. In short, the immense improvement in data and measurement techniques remained dependent on statistics that track sub-populations defined by occupational, provincial and other conventionally pre-determined, closed administrative units. Relations within and between such groups that involve, for example, gender, labour sectors that combine several occupations, and regional cultures and economies, may not be captured accurately in standard administrative units. Subsequent research reanalysing closed data to reflect non-standard units has revealed major fertility differentials and patterns of variation that conventional classifications missed (Szreter 1996; Garrett et al. 2001; Pooley 2013). As evolutionary biologists would expect, population heterogeneity remains strongly characteristic of modern fertility and mortality trends, including the great diversity in patterns of decline. An approach based on *a priori* closed classifications and units has, by itself, not succeeded in establishing the several theories put forward to explain demographic transition, and this problem continues to this day (Cleland and Wilson 1987; Pollak and Watkins 1993; Demeny and McNicoll 2006).

A second major demographic development of the early twentieth century, Lotka's stable population theory, was conceived as a new foundation for the mathematics of evolution. Lotka carried social physics a step further, reasoning that stabilisation in human and molecular populations is analogous, so that the second law of thermodynamics can be used as a model for formal demography. In the *Elements of Physical Biology* (1925), Lotka successfully applied his approach to relations between species, leading to what are now called the Lotka-Volterra equations which provide the basis for studying predator-prey relations. While providing a central and fruitful framework for population ecology, such models address species-level phenomena without attention to intra-species variation, leading Lewontin to remark that they "are both overly specific and arbitrary in their mathematical form so that they may not catch the important reality of interactions" (2004: 15).

More generally, the approach shared some important limitations with Galton and Pearson's work, which have kept it from becoming the general mathematics of evolution that Lotka had hoped to provide. First, because Lotka sets aside the role of intra-species divergence in the renewal of population heterogeneity, his work remained marginal to central debates in evolutionary theory after Mendel, i.e. the problem of how to integrate genetic variation into population thinking, in which heterogeneity arising from environment-organism interactions

remained fundamental. Second, Lotka largely ignored actual processes and variation in organism-environment interaction. Biologists have more recently remarked that the assumption in which the environment acts on the organism as an autonomous force is simply unrealistic: such a view implies that fully formed niches exist waiting for organisms to come to live in them. This assumption is conducive to closed population thinking, since nothing beyond the premise that self-contained environmental units exist in nature is required. Such a view is, however, deeply troubled by evidence that organisms play an active role in constructing niches, so that organisms and environments co-evolve (Lewontin 2001; 2004: 13–16). The same lack of realism arises in human populations if considered in conventional Malthusian terms in which there is a fixed carrying capacity for any environment (Odling-Smee 2015). Reconciling these more recent criticisms with the continuing utility of Lotka's work for population ecology appears to be an ongoing subject of debate.

In the first volume of his principal demographic work, the *Théorie analytique des associations biologiques* (1934), Lotka reiterated the biological foundation of his approach as stated in the *Elements*, together with his careful emphasis, noted earlier, on the purely formal nature of closed analysis. The second volume of the *Théorie* (1939) then developed an extensive application to human populations without reference to other species. Lotka showed how his theory enabled demographers to integrate fertility into the style of analysis used in stationary, or life table, methods, yielding intrinsic growth rates in which purely formal population units, regardless of variation in their initial age/sex structures and vital rates, tend inevitably to stabilise over different time periods. Lotka's later work remained subject to the limitations consequent on exclusively closed population units, just noted.¹¹ Although post-war social demographers (e.g. Ryder 1964) expressed considerable interest in the possibility of developing Lotka's method as a basis for a general sociological theory of population, its limited focus on population renewal, rather than the renewal of population heterogeneity, and its insensitivity to environment-organism interaction, have meant that many sources of variation cannot be integrated into his formal analysis. These commonly remain "independent" economic, cultural and other variables, often analysed via correlation and regression techniques. Thus, although Lotka greatly clarified and subtilized the formal nature of demographic analysis, and did not reduce variation solely to Queteletian normality, the problem of explaining diverse mechanisms of variation and integrating them into models of population stabilisation has remained.

The third major development combining demography and population biology arose in central evolutionary debates over the implications of Mendel's genetic research for Darwinian population thinking. Demographic models were integrated into genetics in Fisher's *Genetical Theory of Natural Selection* (1930), in which he postulated a species in which reproduction occurs continuously in stable age distributions so that, as in (but independently of) Lotka's formulation, life table probabilities and probabilities of birth in a given interval can be combined in a single equilibrium model. Parallel contributions by Wright (1930) and others (see Provine 1971; Lewontin et al. 2003)) moved this approach toward later population genetics by demonstrating the importance of gene or allelic interactions in local populations, encouraging a return to the Darwinian view of species as aggregates of sub-populations (i.e. effective breeding populations, or demes), and of hereditary influence as a consequence of complex interactions

11 In order to treat human populations without reference to their environment, Lotka made a number of further assumptions which have subsequently been disproven (Kreager 2009: 474n)

or combinations of genetic material. This research put a final end to the eugenic quest for simple demographic laws of fitness; rather, while many demographic parameters may combine to shape fitness (e.g. population density; the relative frequency of genotypes, or the mixing of genotypes, in a population) they do so in many different, shifting combinations with other adaptive factors.¹²

Hiatus: the “Separatism” of Demography from Evolutionary Population Biology

All four of the above developments marked an increasing focus of research on fertility and its place in the transmission of characteristics — whether social or genetic — across generations. Without doubt, there was a growing intellectual convergence that brought early twentieth-century demography into closer alignment with evolutionary biology. Yet only the latter participated in the Evolutionary Synthesis that emerged in the 1930s and 1940s, the culmination of half a century of research that brought mathematical modelling of demographic, genetic, cellular and ecological processes into alignment with Darwin’s theory (Mayr and Provine 1998). As the 1950s and 1960s proceeded, no comparable synthesis emerged in the demographic study of human populations, and even demographic followers of Lotka eschewed his evolutionary arguments and applications. Instead, demographers’ growing preoccupation, as is well known, was with theories of demographic transition, in which population biology attained only a secondary role in the biomedicine of mortality and fertility control, and related “proximate determinants”. Evolutionary biology as a major conceptual source of theory and method was strikingly absent when demography’s central post-war concerns came to be established, a neglect that largely continued up to the 1980s (Sear 2015a). The irony, as Lewontin (2004:10) observed, is that once Fisher had put demography at the centre of the genetics of natural selection, evolutionary biology and demography went their separate ways.

Historical accounts have attributed the emergence and powerful influence of separatism to demographers’ aversion to eugenics in the aftermath of national socialism, together with the pressing agenda of post-war reconstruction and fears of rapid population growth. These were indeed important factors, and have been discussed elsewhere.¹³ A more important consideration,

12 Lewontin (2004: 13) describes this as “a lack of transitivity in fitness”: “Competing genotypes can play a game of ‘scissors-paper-stone’ in which genotype A is superior in competition with B and B is superior to C but C is superior to A, because in each competitive interaction a different set of attributes is involved: A is stronger than B, B is faster moving than C and C is more aggressive than A.”

13 The view that separatism arose largely from post-war demographic aversion to eugenics and its preoccupation with rapid population growth, for example in Kreager (2009), neglects four key factors, of which three are evident in the preceding discussion. One is that the GRO’s extensive work to refute eugenics shows that early twentieth-century demographers were already strongly critical. Secondly, eugenicists’ claims that their work was a contribution to Darwin’s theory were unfortunately not refuted adequately by Galton’s contemporaries even though, as we have seen, the fundamental premises of eugenics were a travesty of Darwinian theory. In the absence of such clarification, the confusion of evolutionary approaches with eugenics continued to influence some demographers over the whole first half of the twentieth century, e.g. Pearl (1925). Third, while demographers took Lotka’s mathematics seriously, they jettisoned its evolutionary rationale. We may wonder whether they understood clearly that his biological application concerned ecological issues marginal to central issues in evolutionary debates; again, separatism occurred on the basis of limited awareness relating to a biological sub-field, not with reference to mainstream evolutionary population thinking. In short, the separation of demography and

however, is that the long struggle to construct population genetics and integrate it into Darwin's concept of natural selection had a major impact on how ultimate and proximate causation in evolution are understood. This, in turn, changed the role of mathematical modelling in evolutionary theory in ways consistent with Darwin's work on the divergence of character, but counter to the old Newtonian ideal of theory as a mathematical formalism of ultimate physical relationships. Demographers' non-involvement in the Synthesis meant that few were cognizant of these developments, and that mainstream approaches to population theory and methodology remained, as Hauser and Duncan noted, aligned to physics (1959: 15).

As we have seen, ideas about scientific theory, from Malthus through to Quetelet and Lotka, gave pride of place to the goal inspired by physical sciences of mathematically formulated, general-law-like systems. Darwin was from the beginning sympathetic to this view, and continued to leave open the possibility that statistics could provide methods for modelling the frequency of intra- and inter-species variation. The complexity of open population dynamics, and the "black box" of heredity, however, meant that no formal statistical laws could be put forward in his account of speciation in the *Origin*. In the period from the rediscovery of Mendel to the Synthesis, population genetics employing mathematical methods and closed populations became mainstream in evolutionary thinking, even while commonly seen as opposed to natural historical approaches and the more traditional, predominantly open, Darwinian logic of population thinking. Increasingly, however, the methods developed by Fisher, Wright and others were brought into closer alignment with the observational approaches of natural history and physiology via laboratory research. Species selected for experimentation, like *Drosophila* and small mammals, were chosen because they appeared to open up comparative research on promising hypotheses arising from natural observations (Kohler 1994). Once Mendelian features were established, demes and species populations could then be raised in lab conditions as closed populations for testing purposes, many trials becoming possible because such populations could be reproduced quickly. The role of mathematics in tracking the changing frequencies of genetic characteristics under different mating patterns was to build local models that indicated further hypotheses and tests in which genetic traits and changes could be isolated. The results increasingly moved natural historians and mathematical genetics closer together. On one hand, models such as Fisher's and Wright's established key natural historical arguments, notably that Mendel's results were consistent with Darwinian population thinking. Experiments in natural, as well as laboratory conditions became possible. On the other, mathematical approaches were freed from the nineteenth-century dogma that biological theory should be built primarily along the lines of a physics of ultimate causes. Population genetics could be modelled once mathematics was applied to proximate mechanisms, further removing the dangers that eugenics had exposed in trying to postulate ultimate demographic and genetic laws of evolution. The convergence of approaches also removed, at least for a time, any suggestion of genetic transmission of environmental characteristics, thus helping to focus attention on molecular structure as key to the chemistry of genetic transmission. Watson and Crick's DNA model followed in 1953, and with the rise of genomics, the mathematics of gene sequences can be used to hypothesize and model combinations of genetic chemistry in local parts of the genome that enable laboratory observation and exploration of proximate causes of gene expression.

evolutionary theory was established over the early decades of the twentieth century, and then reinforced by post-war demographic concerns.

Emergent Evolutionary Demography

The approach to general theory in population biology that has emerged from the Synthesis thus remains a methodology that combines insights from closed and open population thinking, not a quest for a universal formalism of evolution. The fundamental open population question, “What is a population?”, still has to be answered whenever the quest is to identify mechanisms of genetic, environmental and phenotypical variation, and this usually requires observation or laboratory construction of local populations (Kreager et al. 2015). The role of formal mathematical approaches, however, has greatly expanded, for example via models that simulate the implications of particular genetic or environmental variations for population composition, structure and change. This is most obviously necessary in the context of genomics: with billions of base pairs, and even more possibly significant combinations of them than persons to which they can belong, the “What is a population?” question becomes “*Which* population?”, i.e. which set of genetic and other parameters, out of the many possible combinations, can be observed to function as proximate causes leading to expression of characteristics that define a population?¹⁴

As Wachter (2015) observes, the route to defining actual populations increasingly proceeds via hypothesized populations. Thus: hypotheses arising from incomplete evidence at higher levels of aggregation in the genome are used to model “local population spaces” in which tests may be carried out, and this activity is likely to precede and accompany successive hypotheses/empirical trials in which key sub-population characteristics are gradually isolated (Lewontin 2004: 17–18). Specifying the population is a critical step in research, and the approach as a whole combines top-down and bottom-up research strategies, as models specifying population characteristics are revised on the basis of each round of evidence.¹⁵ The Synthesis, in short, is not a static paradigm, but has continued to evolve. Evidence, for example, questioning the idea that environmental niches can be modelled simply as closed entities given in nature, has led to reconsideration of Mayr’s ultimate/proximate distinction so that it may better allow for feedback processes (Laland et al. 2010, 2011; Huneman et al. 2017). Such developments are of obvious interest to demography, as they encourage study of how social and cultural relationships are integral to natural selection as part of feedbacks with the genome and the environment.

The recent renewal of demographic interest in evolutionary biology as a source of concepts and models has grown up in this dynamic situation, where the critical role of collaborative research is once again recognised as necessary. On the demographic side, an impetus has also undoubtedly come from the huge problem, noted earlier, of the unexplained heterogeneity of demographic transitions. The “*Which* population?” question here is broadly analogous

14 For example, a population of haemophilia sufferers can be identified on the basis of a single gene, but in the study of cancer or multiple sclerosis the genetic component is much more complex, and there remain serious questions as to environmental influences across the life course which vary between individuals.

15 Spencer (2015) considers the importance of not grouping population members on *a priori* criteria as a concern in current genomic research. While the iterative approach to modelling just described is commonly employed, he remarks on “the unease we have with describing the continuums of diversity of organisms like humans as discrete groups” (2015: 502), and continues by pointing out that if, “in fact, genotype data are available for each individual within the sample [...] why not model each individual as a ‘population’, and let the covariance in alleles between individuals capture the population structure?” (2015: 512). In such a local model space, use of an individual-level correlation matrix avoids having to define populations other than as individual genomes; the set of principal components thus established constitute clines of genetic variation, which may then be explored in a wider sample of individuals. As Spencer says, “every man is an island (or at least a population)” (2015: 512).

to that described for genomics, above. A theory of transition was initially assumed to be universal: modernisation would explain how social, cultural, economic and other proximate causes combine consistently to produce one sequence of reproductive and mortality declines everywhere (allowing, of course, for secondary variations). Instead, an immense heterogeneity of trends within and between societies has been documented, the diversity of which is not consistently explained by the matrix of modernisation variables (see references given in the sub-section on vital statistics, above). In demographers' exploration of alternative approaches, two remarkable parallels to evolutionary biology may be noted.

One is the much greater interest in open population processes, that is, functional links between individuals and between sub-population memberships that are unobserved in standard demographic classifications and closed population units. These include: the impact of hierarchical relations on inequalities in demographic outcomes; inter-generational relationships and variation of generational roles across the life course as they affect reproduction, family formation and longevity; migration and changing cultural identities as adaptive strategies; and network transmission of ideas and practices between sub-populations as they shape varying reproductive choice and health outcomes within and between groups. The second and related development is increasing attention to sub-population variation at levels below, or that cut across, conventional national and provincial administrative population units. Current problems of demographic explanation, in other words, have drawn the field toward the kinds of issues that long ago, in Classical population thinking, gave relationships between sub-populations and their members a determinant role, and which likewise shaped Darwin's account of how demes and species are formed and change.

By way of conclusion, two brief examples drawn from recent evolutionary demography can be used to illustrate how the methodology of local population spaces described above is now being used to address central problems of demographic explanation. As Kaplan and Gurven (2008) reiterate, combined top-down and bottom-up population thinking is necessary. Bottom-up approaches may, for example, relate physiological variables (e.g. mothers' energy reserves as indicated by body mass index (BMI); dietary constraints; local environmental disease risks to infants) to demographic measures (mothers' age at first birth, parity progression, infant mortality) in order to identify proximate causes as they vary health conditions and changing vital rates in different sub-populations. The top-down element is provided by life history theory: reproduction entails trade-offs in which available parental energy and resources for childrearing must be balanced against the increasing demands that a succession of children inevitably makes; natural selection occurs as interactions between physiological constraints and the incidence of births and infant deaths alter this balance in ways that regulate continuing parental investments and the survival of certain children. Note that this approach, rather than treating fertility and mortality separately, focusses on feedback mechanisms between them in specific environments. Modernisation variables act not as external forces that sweep away traditional arrangements, but through this proximate process, and they may be more or less important depending on which aspects of environment-organism-genetic interaction they influence.

Longitudinal research on Tsimane communities in Bolivia provides an example of a "bottom-up" study, addressed to lowland, subsistence farming and foraging communities whose way of life and demography remain substantially traditional (Kaplan et al. 2015). A combined ethnographic methodology incorporates continuing comprehensive census data

collection, reproductive history interviewing and annual medical examination of a wide range of physiological characteristics. This combination provides local population data from several observational techniques which can be compared and analysed as an effectively closed population. Total fertility is at very high pre-transition levels (8.8 births per woman), with modestly lower rates in communities somewhat more exposed to Bolivian towns. Although the latter communities now have greater access to public health facilities, infant mortality levels have risen, even while women's BMI has improved. The authors show how this rather counter-intuitive pattern can be accounted for by linking reproductive histories to women's improved energy circumstances: births have come at earlier ages in marriage, and closer together, both of which are facilitated by higher energy resources, but which normally carry added health risks. Variables that might be expected indicate modern impacts, like education and greater facility in speaking Spanish, appear to have at most minor influence. In the authors' view, this finding shows the operation of natural selection as maximising the production of surviving offspring (i.e. not maximised fertility) in balance with the realities of parental investment.

The study is prospective in the sense that the Tsimane communities are at a pre- or initial stage of demographic transition: the authors, expecting fertility declines to ensue, have established a baseline of current proximate mechanisms and their relationships on which subsequent variations in familial, physiological and community-level factors and their interactions can be assessed. Such baselines have been notably absent in most transition research. Their finding that mothers' age declines at first birth, associated with higher overall levels of fertility, is already indicative of a central mechanism of "pre-decline rise" in the region, and is one of the main lacunae to have been found in transition theory (Dyson and Murphy 1985). Their approach, in considering feedbacks between fertility and mortality via physiological factors, also runs counter to conventional transition and Malthusian arguments that higher fertility is a homeostatic response to higher mortality. While community variables like education and bilingualism are not yet important influences, as components of social learning they are likely to become a potentially major environmental force in social and genetic change (Sears 2015b). The authors underline the importance of ethnography at sub-population levels in evolutionary demography, noting that subsequent research will need to identify the social networks in which health information associated with these variables may spread more widely.

The second example takes up the question of how such social relationships can be integrated into formal modelling of evolutionary change. As noted earlier, one of the problems demography has faced is how to bring variation in social and economic relationships, or "independent" variables, into core demographic analysis. The issue is thus one of preparing new top-down approaches. Lee (2003, 2008), for example, has addressed the role of inter-generational transfers as a mechanism of evolutionary demography, with particular reference to ageing and juvenile mortality. Conventional evolutionary models, following Hamilton (1966), rest on a purely demographic analysis in which, under a stable population growth rate, mortality increases at older ages in inverse relation to expected fertility by age. Put very simply: as older people do not have babies, their contribution to group fitness may appear to be marginal; further, if they have no proximate functions supporting fertility, and are susceptible to the complications of age-specific deleterious mutations as they reach later life, there would seem to be no serious evolutionary advantage to their increased longevity.

As Lee remarks, this formulation leaves the human capacity for long post-reproductive survival unexplained.¹⁶ A considerable body of natural historical, ethnographic and historical evidence has for some time made the conventional view untenable: elders, particularly female relatives, contribute substantial support to raising their grandchildren, and in many cases to others in younger generations that are not direct descendants. As proximate functions of support contributed by elders to the survival and growth of groups are evident in many species, selection for their greater longevity (including differences for the sex contributing most to transfers) is logically indicated. Likewise, the uniform progression of mortality with age in the conventional model, by not taking account of transfers, fails to recognise that early death, e.g. in infancy, incurs much less physiological and support cost than deaths at juvenile ages, by which time much greater investments have been made.

Life history theory, in which a balance between fertility, mortality and investments in children is fundamental to evolution, again provides the elemental logic. Lee's model is addressed to the long period from prehistory in which the human race depended on foraging, so again a kind of baseline is being established. As the objective is to show what difference transfers make to levels of fertility, mortality and natural increase at each age across the life course, a complex set of variables is entailed. Since production varies with a group's relative success in competition for food and resources, the capacity to make transfers depends on population density and size. Production also depends on feedbacks from consumption, since it depends on the growth, size and strength of individual members, which have been shaped by the food and resources available to them. The net transfer that becomes possible at each age can therefore be modelled as estimated production minus consumption (assuming no wastage); this will vary according to the composition of units or groups involved, and Lee's model may be applied to a range, from individuals and mother-offspring sets to larger family groups and cooperative breeding groups. The implications for natural selection then turn on how changes in fertility and mortality, and resulting age structures, interact with intergenerational investment supported by transfers. Lower mortality at the youngest ages increases population growth, and, if coupled with lower mortality at older ages, profits from feedbacks via transfers that also optimise longevity, further stimulating population increase. Greater surviving reproduction thus increases fitness at both the top and the bottom of the age pyramid; transfers become the key to understanding longer post-reproductive longevity characterising more successful and numerically dominant competitive groups. For these groups with greater capacity to invest in children who are then more likely to survive, older adults over time will come increasingly to be selected genetically for greater longevity — this not only helps to ensure continued transfers, but opens up the possibility of reducing fertility (i.e. increasing the quality and quantity of investment per child), thus avoiding the Malthusian trap of high density groups becoming subject to too much competition. As every unit must be in transfer balance (whether successfully, or via loss of

16 Beginning in the 1960s, two distinguished British evolutionary biologists, William Hamilton and Brian Charlesworth, developed models of ageing that relate genetic variation to life history, and which have substantially reshaped understanding of variation in longevity and its relation to fecundity. Further discussion of Hamilton can be found in Ronald Lee's chapter, 'Sociality, Food Sharing and the Evolution of Life Histories', and of Charlesworth in Ken Wachter, 'Genetic Evolutionary Demography', both in this volume.

members to mortality at younger and older ages), the sum of all units, or the total population, will also be in balance.

In its early formulation, Lee's model made a number of abstract assumptions, for example only applying to single-sex transfers of food in stable populations. Later iterations have reduced some of these, and also included more variables, but an account here would extend discussion greatly beyond the scope of this chapter. In each case the model has been developed with evidence from the ethnographic background on foraging populations in mind, and applied to population data on them. Simulations utilising the model enable a 75,000-year prehistory of foraging groups to be constructed, a picture of environment-organism-genetic interaction in the long term. This may, as further developed, serve as a baseline indicating possible ultimate evolutionary parameters within which proximate mechanisms — introduced in the relatively short and recent 2,000-year period of more complex agricultural, urban and manufacturing societies — can be understood.

Concluding Note

In view of the historical development of population thinking traced in this chapter, it is clear that research has moved on from the hunt for ostensible laws of natural selection based, for example, on Malthus's positive check in closed populations, or the eugenics of reproductive selection. The Evolutionary Synthesis, in reasserting Darwin's dual conceptualisation of population thinking, has facilitated a closer relation between formal modelling and local population data, whether in laboratory or field settings, and increasingly in the later twentieth century with reference to proximate processes observed in human groups. Stepping back from this long and complex history, the importance of evolutionary population biology to demography may be summarised broadly on two counts.

One, as we have seen, is to remind demographers of the substantial body of population theory on which social and biological population research *jointly* rest. Darwin, in building his theory of evolution on analogy between observation-based natural history and Smith's account of the division of labour, enabled evolutionary biology to remain truer to the long tradition of open population thinking than has been the case in demography, with its overriding focus on closed methodologies of population statistics. Demography over the nineteenth and twentieth centuries remained primarily the study of population renewal, whereas evolutionary biology has addressed both renewal and structural change by explaining the dynamics that renew population heterogeneity. Yet Darwin, in also insisting on the crucial role of statistical demonstration of the variation and divergence of characteristics, opened the door to applications of actuarial methods, which early-twentieth-century analysts like Lotka, Fisher, Galton and Pearson then began to develop. Recognition of the complementarity of the two concepts of population was one of the main achievements of the Synthesis.

A second wider implication of this history follows from the fact that mid-twentieth-century social and economic demography did not undergo a comparable synthesis. Its approach to theory, notably in attempts to explain demographic transitions, remained focussed primarily on the evidence of closed population methods, often viewed in terms of stylised macro- and micro-levels. This methodology has undoubtedly proven very fruitful in tracking aggregate trends at these levels. The central finding of a vast body of research on demographic transitions has been to demonstrate the immense heterogeneity of fertility and mortality declines in the modern

era, taking place in a vast array of environments — exactly as Darwinian population thinking would lead us to expect. However, in its reliance on closed units, often based on institutional compilations rather than sustained observation of groups in society, and without a primary focus on evolving interdependence and divergence amongst constituent populations, demography has encountered great difficulty in providing a scientific explanation of its central finding. Evolutionary demography, following on from population biology, recognises that heterogeneity requires explanation on several levels, from genetic and cellular processes up to the diverse ways in which social groups are distributed and redistributed in social structures over time.¹⁷ Formal population analysis remains by definition addressed to closed units, but its development is shaped necessarily by increasingly complex bottom-up configurations of observed proximate mechanisms — the “division of labour” within and amongst local populations which Darwin recognised as the locus of environment-organism-genetic evolution.

References¹⁸

- Browne, J. 1980. ‘Darwin’s Botanical Arithmetic and the “Principle of Divergence”, 1854–1858’, *Journal of the History of Biology* 13.1: pp. 53–89, <https://doi.org/10.1007/bf00125354>
- Cleland J. and C. Wilson. 1987. ‘Demand Theories of Fertility Transition: an Iconoclastic View’, *Population Studies* 41.1: pp. 5–30, <https://doi.org/10.1080/0032472031000142516>
- Darwin, C. 1851. *A Monograph on the Subclass Cirripedia* (London: The Ray Society).
- . (1868). *The Variation of Animals and Plants under Domestication*, I-II (London: Murray).
- (1958), *The Autobiography of Charles Darwin*, N. Barlow (ed.). (London: Collins).
- . 1996 [1859]. *The Origin of Species* (Harmondsworth: Penguin).
- Demeny, P. and G. McNicoll. 2006. ‘World Population 1950–2000: Perception and Response’, in *The Political Economy of Global Population Change, 1950–2050, Population and Development Review Supplement*, 32: pp. 1–51, New York: The Population Council, <https://doi.org/10.1111/j.1728-4457.2006.tb00002.x>
- Dyson, T. and M. Murphy. 1985. ‘The Onset of Fertility Transition’, *Population and Development Review*, 11.3: pp. 399–440, <https://doi.org/10.2307/1973246>
- Fisher, R. A. 1930. *The Genetical Theory of Natural Selection* (Oxford: Clarendon Press).
- Flew, A. 1982. ‘Introduction’, in T. R. Malthus, *An Essay on the Principle of Population* (Harmondsworth: Penguin).
- Galton, F. 1907. ‘Probability, the Foundation of Eugenics’, *The Popular Science Monthly*, 71: pp. 165–78, <https://doi.org/10.2307/2331694>
- Garrett, E., A. Reid, K. Schürer, and S. Szreter. 2001. *Changing Family Size in England and Wales, 1891–1911* (Cambridge: Cambridge University Press).
- Gould, S. J. 2002. *The Structure of Evolutionary Theory* (Cambridge, Mass.: Harvard University Press).
- Hamilton, W. E. 1966. ‘The Moulding of Senescence by Natural Selection’, *Theoretical Population Biology*, 12: pp. 12–45, [https://doi.org/10.1016/0022-5193\(66\)90184-6](https://doi.org/10.1016/0022-5193(66)90184-6)

17 Exploration of alternative levels of analysis and their implications for explanatory models are a subject of the many contributions to Kreager et al. 2015.

18 Note this chapter has been posted on the Open Science Framework website since 13/06/2019, after it was accepted for publication, so the references will reflect when the chapter was written and not the OBP publication date.

- Hauser, P. M. and O. D. Duncan. 1959. 'Overview and Conclusions', in *The Study of Population: An Inventory and Appraisal*, ed. by P. M. Hauser and O. D. Duncan (Chicago: University of Chicago Press), pp. 1–117.
- Huneman, P. and D. M. Walsh. 2017. *Challenging the Modern Synthesis* (Oxford: Oxford University Press).
- Kaplan, H. and M. Gurven. 2008. 'Top-Down and Bottom-Up Research in Biodemography', *Demographic Research*, 19, 44: pp. 1587–1602, <https://doi.org/10.4054/demres.2008.19.44>
- Kaplan, H., P. L. Hooper, J. Stieglitz, and M. Gurven. 2015. 'The Causal Relationship between Fertility and Infant Mortality: Prospective Analyses of a Population in Transition', in *Population in the Human Sciences: Concepts, Models, Evidence*, ed. by P. Kreager, B. Winney, S. Ulijaszek and C. Capelli (Oxford: Oxford University Press), pp. 361–78, <https://doi.org/10.1093/acprof:oso/9780199688203.003.0013>
- Kohler, R. E. 1994. *Lords of the Fly: Drosophila Genetics and the Experimental Life* (Chicago: University of Chicago Press).
- Kreager, P. 1988. 'New Light on Graunt' *Population Studies*, 42.1: pp. 129–40, <https://doi.org/10.1080/00324720.31000143156>
- . 2008. 'Aristotle and Open Population Thinking', *Population and Development Review*, 34.4: pp. 599–629, <https://doi.org/10.1111/j.1728-4457.2008.00243.x>
- . 2009. 'Darwin and Lotka: Two Concepts of Population', *Demographic Research*, 21.16: pp. 469–502, <https://doi.org/10.4054/demres.2009.21.16>
- . 2014. 'On the History of Malthusian Population Thought', *Population and Development Review*, 40.4: pp. 73–742, <https://doi.org/10.1111/j.1728-4457.2014.00009.x>
- . 2015. 'Population and the Making of the Human Sciences: A Historical Outline', in *Population in the Human Sciences: Concepts, Models, Evidence*, ed. by P. Kreager, B. Winney, S. Ulijaszek and C. Capelli (Oxford: Oxford University Press), pp. 55–85.
- . 2017. 'Adam Smith, the Division of Labour, and the Renewal of Population Heterogeneity', *Population and Development Review*, 43.3: pp. 513–39, <https://doi.org/10.1111/padr.12085>
- Kreager, P., B. Winney, S. Ulijaszek and C. Capelli, (eds.). 2015. *Population in the Human Sciences: Concepts, Models, Evidence* (Oxford: Oxford University Press).
- Laland, K. N., J. Odling-Smee, S. Myles. 2010. 'How Culture Shaped the Human Genome: Bringing Genetics and the Human Sciences Together', *Nature Reviews/Genetics*, 11: pp. 137–49, <https://doi.org/10.1038/nrg2734>
- Laland, K. N., K. Sterelny, J. Odling-Smee, W. Hoppitt, T. Uller. 2011. 'Cause and Effect in Biology Revisited: Is Mayr's Proximate-Ultimate Dichotomy Still Useful?', *Science*, 334: pp. 1512–16, <https://doi.org/10.1126/science.1210879>
- Lee, R. 2003. 'Rethinking the Evolutionary Theory of Ageing: Transfers, Not Births, Shape Senescence in Social Species', *Proceedings of the National Academy of Sciences of the United States of America*, 100.16: pp. 9637–42, <https://doi.org/10.1073/pnas.1530303100>
- . 2008. 'Sociality, Selection and Survival: Simulated Evolution of Mortality with Intergenerational Transfers and Food Sharing', *Proceedings of the National Academy of Sciences of the United States of America*, 105.20: pp. 7124–28, <https://doi.org/10.1073/pnas.0710234105>
- Lewontin, R. 2001. *The Triple Helix: Gene, Organism and Environment* (Cambridge, Mass.: Harvard University Press).
- . 2003. 'Introduction: The Scientific work of Theodore Dobzhansky', in *Dobzhansky's Genetics of Natural Populations I–XLIII*. Ed. by R. C. Lewontin et al. (New York: Columbia University Press), pp. 93–115.
- . 2004. 'Building a Science of Population Biology', in *The Evolution of Population Biology*, ed. by R. S. Singh and M. K. Uyenoyama (Cambridge: Cambridge University Press), pp. 7–20.
- Limoges, C. 1968. 'Darwin, Milne-Edwards, et le principe de divergence', *XII Congrès International d'Historire des Sciences*, pp. 111–15.

- . 1970. *La sélection naturelle: Étude sur la première constitution d'un concept, 1837–1859* (Paris: Presses Universitaires de France).
- Lotka, A. 1925. *Elements of Physical Biology* (Baltimore: Williams and Wilkins).
- . 1934, 1939. *Théorie analytique des associations biologiques I, II* (Paris: Herman et Cie).
- Malthus, T. R. 1982 [1798]. *An Essay on the Principle of Population* (Harmondsworth: Penguin).
- Mayr, E. 1961. 'Cause and Effect in Biology', *Science* 134:1501–06, <https://doi.org/10.4324/9781315133638-2>
- . 1982. *The Growth of Biological Thought* (Cambridge, Mass: Belknap Press).
- . 2004. *What Makes Biology Unique? Considerations on the Autonomy of a Scientific Discipline* (Cambridge: Cambridge University Press).
- Mayr, E. and Provine, W. B. (eds.). 1988. *The Evolutionary Synthesis: Perspectives on the Unification of Biology* (Cambridge, Mass.: Harvard University Press).
- Milne-Edwards, H. 1827. 'Organisation', in *Dictionnaire classique d'histoire naturelle*, XII, pp. 332–44.
- . 1851 [1834]. *Introduction à la zoologie générale, ou, Considérations sur les tendances de la nature dans la constitution du règne animal* (Paris: Masson), <https://www.biodiversitylibrary.org/item/148268#page/9/mode/lup>
- Odling-Smee, J. 2015. 'Niche Construction in Human Evolution and Demography', in *Population in the Human Sciences: Concepts, Models, Evidence*, ed. by P. Kreager, B. Winney, S. Ulijaszek and C. Capelli (Oxford: Oxford University Press), pp. 147–71.
- Pearl, R. 1925. *The Biology of Population Growth* (New York: Knopf).
- Pearson, K. 1896. 'Contributions to the Mathematical Theory of Evolution: Note on Reproductive Selection', *Journal of the Royal Statistical Society* 59, 2: 398–402, <https://doi.org/10.1098/rspl.1895.0093>
- . 1912. *The Problem of Practical Eugenics*, London: Dulau and Co.
- Pollak, R. A., and S. C. Watkins. 1993. 'Cultural and Economic Approaches to Fertility: Proper Marriage or *Mésalliance*?', *Population and Development Review*, 19.3: pp. 467–96, <https://doi.org/10.2307/2938463>
- Pooley, S. 2013. 'Parenthood, Child-Rearing and Fertility in England, 1850–1914', *History of the Family*, 18.1: pp. 83–106, <https://doi.org/10.1080/1081602x.2013.795491>
- Porter, T. M. 1986. *The Rise of Statistical Thinking, 1820–1900* (Princeton: Princeton University Press).
- Provine, W. B. 1971. *The Origins of Theoretical Population Genetics* (Chicago: University of Chicago Press).
- Quetelet, A. 1869. *Physique Sociale*, I-II (Brussels: C. Muquardt).
- Ryder, N. B. 1964. 'Notes on the Concept of a Population', *American Journal of Sociology*, 66.5: pp. 447–63, <https://doi.org/10.1086/223649>
- Schweber, S. S. 1977. 'The Origin of the Origin Revisited', *Journal of the History of Biology*, 10.2: pp. 229–316, <https://doi.org/10.1007/bf00572644>
- . 1980. 'Darwin and the Political Economists: Divergence of Character'. *Journal of the History of Biology*, 13: pp. 195–289, <https://doi.org/10.1007/bf00125744>
- Sear, R. 2015a. 'Evolutionary Demography: A Darwinian Renaissance in Demography', in *International Encyclopedia of the Social and Behavioral Sciences*, ed. by J. D. Wright, 2nd edition, VIII (Oxford: Elsevier), pp. 406–12.
- . 2015b. 'Evolutionary Contributions to the Study of Human Fertility', *Population Studies*, 69.S1: pp. 39–55, <https://doi.org/10.1080/00324728.2014.982905>
- Smith, A. 1976 [1776]. *An Inquiry into the Nature and Causes of the Wealth of Nations*, ed. by R. H. Campbell and A. S. Skinner, W. B. Todd (text ed.), I-II (Oxford: Clarendon Press).
- Soloway, R. A. 1982. *Birth Control and the Population Question in England 1877–1930* (Chapel Hill: University of North Carolina Press).

- Spencer, C. 2015. 'From Populations to Clines in Modern Statistical Genetics', in *Population in the Human Sciences: Concepts, Models, Evidence*, ed. by P. Kreager, B. Winney, S. Ulijaszek and C. Capelli (Oxford: Oxford University Press), pp. 501–16.
- Szreter, S. R. S. 1984. 'The Genesis of the Registrar-General's Social Classification of Occupations', *British Journal of Sociology*, 35.4: pp. 522–46, <https://doi.org/10.2307/590433>
- . 1996. *Fertility, Class and Gender in Britain, 1860–1940* (Cambridge: Cambridge University Press).
- Wachter, K. 2015. 'Population Heterogeneity in the Spotlight of Biodemography', in *Population in the Human Sciences: Concepts, Models, Evidence*, ed. by P. Kreager, B. Winney, S. Ulijaszek and C. Capelli (Oxford: Oxford University Press), pp. 131–45.
- Wrigley, E. A. 1986. 'Elegance and Experience: Malthus at the Bar of History', in *The State of Population Theory: Forward from Malthus*, ed. by D. Coleman and R. Schofield (Oxford: Blackwell), pp. 46–64.
- Wright, S. 1930. 'The Genetical Theory of Natural Selection. A Review', *Journal of Heredity*, 21: pp. 349–56, <https://doi.org/10.1093/oxfordjournals.jhered.a103361>