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Migration and colonization in human microevolution

Migration and colonization are major forces affecting the frequency, spatial pattern and spread of genes in human populations. Here, Alan Fix reviews theories of migration developed by biologists and social scientists, and surveys patterns of migration in a diverse sample of human populations. Using these empirical studies, he evaluates models of migration developed by population geneticists and explores more realistic models using computer simulation. He then shows the relevance of studies of migration as a microevolutionary process to the understanding of longer term global patterns of human diversification, by examining the spread of anatomically modern *Homo sapiens*, the demic diffusion of agriculture in Europe, and the origins of human diversity in the Malayan Peninsula. By focusing on migration as a process rather than as its genetic consequences, the book provides a bridge between biological and social science studies of migration, genetic microevolutionary theory and longer term human evolution.

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CAMBRIDGE
UNIVERSITY PRESS

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK   www.cup.cam.ac.uk
40 West 20th Street, New York, NY 10011-4211, USA   www.cup.org
10 Stamford Road, Oakleigh, Melbourne 3166, Australia
Ruiz de Alarcón 13, 28014 Madrid, Spain

First published 1999

Printed in the United Kingdom at the University Press, Cambridge

Typeface Times 10/12.5pt [VN]

A catalogue record for this book is available from the British Library

Library of Congress Cataloguing in Publication data

Fix, Alan G.
Migration and colonization in human microevolution / Alan G. Fix.
p.   cm. – (Cambridge studies in biological and evolutionary anthropology)
Includes bibliographical references and index.
ISBN 0 521 59206 2
1. Human population genetics.   2. Emigration and immigration.
3. Human evolution.   I. Title.   II. Series.
Gn289.F59   1999
304.8 dc21   98-32340   CIP

ISBN 0 521 59206 2 hardback

To Betsy, Aaron, and Amy

Contents

Preface xi
Plan of the book xiii
Acknowledgments xvii

1 The study of migration 1
Evolutionary and ecological perspectives 1
  Definitions and patterns: migration, dispersal, and gene flow 1
  Population structure: units of analysis 2
  Causal models 2
Social science perspectives 6
  Demographic models 6
  Geographic and economic models 8
Anthropological genetics: integration of social and biological perspectives 12

2 The anthropology of human migration 13
Dimensions of diversity in cultural and ecological circumstances 13
  Low population density, extensive land use, family groups 17
    Australia – Yolgnu 17
    South Africa – !Kung San 23
    Central Africa – Aka 25
  Low to moderate density, extensive cultivators, local kin groups 28
    Lowland Amazonia – Vaupés 28
    Lowland Amazonia – Yanomamo 30
    Malaysia – Semai Senoi 33
    New Guinea – Gainj–Kalam 36
  High density, intensive agriculturalists, local groups within state 39
    Spain – Basque (1850–1910) 39

England – Oxfordshire (1851) 42
Northern India – Faizabad District (1951) 45
Generalizations 47

3 Population genetics models and human migration 51
Classic models 51
The island model 52
Isolation by distance 53
Malécot's isolation by distance 54
The stepping-stone model 59
Migration matrix model 61
Neighborhood knowledge model 67
Basic variables 74
Life cycle timing 75
Units 78
Kin structure 79
Spatial pattern 90
Geography and distance 90
Population sizes 92

4 Computer simulation models 94
Experimental approaches to history and the interaction of evolutionary forces 94
Minimum endogamous population size 95
Interaction of genetic drift and migration – kin-structured migration (KSM) 106
Migration–selection interaction – detecting clinal and balanced selection under KSM 111
Wave of advance of advantageous gene 120
Colonization with founder effect – clines 130
Colonization with extinction – structured demes in metapopulations 136

5 Migration and colonization in human evolution 149
Initial spread of *Homo sapiens* 153
Mitochondrial DNA 153
African homeland: evidence and arguments 155
Demic diffusion of agriculture through Europe 168
The demic diffusion model 169
Genetic patterns in Europe 171
Temporal selection model 172

Cambridge University Press
0521592062 - Migration and Colonization in Human Microevolution
Alan G. Fix
Frontmatter
More information

Evaluation of the models 175
Prehistoric Southeast Asian dispersals: Peninsular Malaysia 182
Cultural traditions in Peninsular Malaysia 186
Biological origins of the Orang Asli 190
Population units in historical analysis 192
Hemoglobin E, ovalocytosis, and history in Southeast Asia and Near Oceania 199

6 Conclusions: an evolutionary framework for the study of migration 203
Behavioral ecology of migration 205
Anthropology of human migration 206
Population genetic models of migration 207
More complex models – computer simulation 209
Migration and colonization in the long term 211

References 215
Index 233

Preface

This book is about the role of migration and colonization as agents in human microevolution; that is, how human spatial displacements affect the frequencies, pattern, and spread of genetic variants in human populations. My approach is from anthropological genetics: anthropological in that patterns of mating, technologies and economies, and social structures are cultural attributes of populations that profoundly influence migration; genetic in that it is the biologically significant effects of migration on genetic structure that are to be understood.

The study of migration ranges across the territory of several disciplines, from biology and evolutionary genetics to the social sciences, including cultural anthropology, archaeology, demography, and geography.

In biology, migration (or gene flow) is one of the four forces of evolution along with mutation, natural selection, and genetic drift, and plays an important role in the general theory of evolutionary genetics (Wright 1931). Migration is also a major topic in ecology both as a phenomenon to be understood (Dingle 1996) and as a variable in the relationship between social and genetic structures (Chepko-Sade & Halpin 1987).

In the social sciences, geographers, with their focus on spatial relationships, have been at the forefront of migration research (Clark 1986; Lewis 1982; Robinson 1996). Migration has always been an important explanatory concept for archaeologists. Recently this interest has intensified (Anthony 1990) and colonization has been raised to the central issue of human prehistory by Gamble (1994) in his book, *Timewalkers: the Prehistory of Human Colonization*. Such explanations have a venerable history in cultural anthropology as well (recall the various ‘historical schools’ of anthropology active in the early part of the century (Lowie 1937)).

In human genetics, the rapid proliferation of molecular ‘markers’ in recent years has stimulated efforts to trace routes of migration and colonization. Global questions of human ancestry from the initial spread of our species (Cann *et al.* 1987) to new hypotheses for the peopling of the New World (Wallace & Torroni 1992) and the colonization of Oceania (Serjeantson & Hill 1989) and the demic diffusion of agriculture through

Europe (Ammerman & Cavalli-Sforza 1984) have been addressed using both molecular and 'classical' genetic data. Perhaps the most ambitious of these studies has been the global survey of gene distributions by Cavalli-Sforza and his colleagues (1994); the predominant explanation offered for these patterns in this work is population fission, migration, and isolation.

The fundamental problem for all reconstructions that assume migration as a cause, however, is how to distinguish past population movements from other processes that lead to the same distributional outcomes. More particularly, how do present distributions of artifacts, languages, or gene 'markers' signify movement of people as opposed to other processes such as cultural diffusion or transformation (in the case of genes or natural selection)? For this reason, the definitive demonstration of any prehistoric movement must depend on multiple converging lines of evidence.

Critical to this demonstration must surely be the understanding of the *process* of movement (Madsen & Rhode 1994). The comparative study of migration in the contemporary world is the primary source for a causal theory of migration. This is not to say that conditions in the distant past could not have been so different that no modern analog would apply; however, a *theory* of migration specifying the variables and conditions affecting rates and patterns of migration should provide guidance for assessing models of past population movement. The primary sources for this theory are the large literature from anthropological genetics documenting comparative population structures and mobilities (e.g., Boyce 1984; Crawford & Mielke 1982; Harrison & Boyce 1972b; Little & Leslie 1993; Mascie-Taylor & Boyce 1988) and the ethnographic record documenting covariation between socio-ecological variables, population properties, and movement (Johnson & Earle 1987).

My aim in this book is to survey this literature, looking for patterns and regularities among the diversity of cultures and population structures recorded by anthropologists, and attempting to identify key variables affecting gene distributions. A general theory of migration must be able to encompass the full range of human mobilities, from the extreme local sedentism found in some small-scale agrarian societies to the mass migrations of recent times. Such a comprehensive theory would require enlarging of the scope of classic genetic models to include a greater diversity of population structures. Simple patterns of nearest neighbor exchange or continent to island gene flow capture only a portion of this diversity. More complex models, such as those made possible by computer simulation, allow experimentation with a greater range of population structures and migration patterns. While I cannot claim to have developed a general model in this book, I have tried to suggest ways to broaden our view of the role of migration and population structure in human microevolution.

The title of a paper by John Moore (1994), ‘Putting anthropology back together again’, nicely captures my orientation in this work. For much of its history, anthropology constituted a kind of ‘natural historical’ study, integrating data and questions from biology to art. Current trends seem to be toward more specialization and fragmentation of the subdisciplines. A microscope gives a very clear picture of a very small field. If we are still to be concerned with global questions of human diversity and evolution, too narrow a focus blinds us to this broader picture. To know everything about potsherds (or the mitochondrial genome) and little about people does not seem a good strategy to understand human populations. Such understanding is more likely with the exchange of information across disciplinary (or subdisciplinary) lines along with efforts to synthesize these data and interpretations.

The dilemma of synthesis is to venture into fields where one is not expert on the one hand, and to fail to communicate to experts in fields other than one’s own on the other. I hope to have avoided major mistakes in areas where I have little technical expertise. I have also tried to avoid jargon and excessive equations. Although the book is primarily intended for anthropologists and human geneticists, I would also be gratified if biologists interested in broad patterns across taxa (Dingle 1996) might be made aware of the scope of detailed data on migration in human populations from anthropological and historical sources.

Plan of the book

The first chapter surveys the perspectives of the different disciplines concerned with the study of migration and provides definitions of basic terms and an introduction to causal models. This discussion provides a general context for the anthropological and genetic study of migration in the remainder of the book.

Human populations throughout history have varied enormously in size, density, and structure, reflecting their diverse cultural and ecological circumstances. Chapter 2 begins with a sketch of the techno-economic variation among human populations and its implications for population densities and migratory patterns. The principal factor implicated in this diversity is the degree of intensity of land use required by the technology of the population which is also correlated with population density and degree of social integration. Using these variables as dimensions of comparison, a

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Alan G. Fix
Frontmatter
More information

series of anthropologically well-known case studies are presented. These represent points on a continuum of populations from low-density, highly mobile, politically autonomous families or local groups, through swidden-farming village-level polities, to more densely settled farmers organized into regional political entities and include:

(1) Classic mobile hunter–gatherers showing flexible group structure and wide ranging kin ties resulting in large interacting population networks. Examples discussed in Chapter 2 are Australian Aboriginal groups (mainly the Yolgnu of Arnhem Land), the !Kung San of the South African Kalihari Desert, and the central African forest Aka pygmies.
(2) More sedentary collectors with higher population densities and more localized groups. Examples of this category would include the Northwest Coast-California Indians (and maybe Mesolithic Europeans). Unfortunately, this group of societies has not received the detailed study devoted to the more mobile foragers, and therefore no examples have been included. Because most of these societies occupied lands that were attractive to farmers, few of them persisted to be documented by anthropologists.
(3) Small scale agricultural societies with population densities no higher than the settled collectors of category 2 and practicing extensive land use techniques (swiddens). Politics is local in these societies; villages are usually autonomous and subject to periodic group fission and fusion. Examples considered in Chapter 2 are Amerindian groups of the Vaupés region of Columbia and the Venezuelan Yanomamo and the technologically similar societies of the Malaysian Semai Senoi and the Gainj of Papua New Guinea.
(4) More intensive agriculturists with higher population densities, larger political groups including state organization and social stratification. The societies representing this category discussed in Chapter 2 are all examples of what are often called ‘peasants’; that is, rural agrarian peoples within the borders of nations. They include the Basque farmer/herders of the French–Spanish border region, rural parishes in Oxfordshire, England and a subdistrict in Uttar Pradesh, northern India.

For each case, the factors affecting migration will be examined and special issues illustrated by the case will be detailed (e.g., the role of inheritance patterns in Basque migration). The rationale for considering these different cultures and economies is to assess the extent of variation in human migratory patterns and its relevance to genetic models.

The aim in Chapter 3 is to characterize the classic population genetics models of migration and population structure. These include the island, isolation by distance, stepping-stone, migration matrix, and neighborhood knowledge models. The survey is not exhaustive nor very mathematical (see Jorde, 1980, for a detailed review), but rather focuses on the underlying migration patterns that these models are attempting to capture. The strengths and weaknesses of these models are evaluated in light of the previous discussion of the pattern and structure of human migration and, for several, case studies are examined as focused examples. A set of basic variables is identified and considered, including: (1) stage of the life cycle at which migration occurs, whether pre-marital, marital, or post-marital; (2) the units of migration, whether gametes or individuals along a continuum to population fission and group migration; (3) the structure of migrant groups (random or kin); (4) the spatial pattern of migration varying from exchange between nearest neighbors along a continuum to long distance displacements; (5) geographic structure and distance; and (6) population size.

Chapter 4 continues the discussion of population genetics and migration now focused on computer simulation modeling, a method allowing a more detailed exploration of some of the variables identified in Chapter 3 (for example, the role of kin-structured migration was first studied using simulation techniques). Evolution, as Sewall Wright long maintained, is an interaction of forces; gene frequency change is often the joint outcome of several processes operating concurrently. Particularly in the small populations studied by anthropologists, these processes are subject to random variation. Computer simulation allows these more complex interactions and stochastic variation to be modeled. In a broader sense, simulation can be viewed as an 'experimental' technique to study history. In the absence of time machines, we can't turn back the clock to see what happened in evolution. We can, however, replicate processes under controlled conditions using computer simulation and see what might have happened.

Several examples of stochastic simulation models incorporating the interaction of migration with other forces of evolution are presented, including the effect of kin-structuring of migration (KSM), the interaction of clinal and balanced selection with KSM, the wave of advance of an adaptive allele, the potential role of colonization and founder effect in producing genetic clines, and the interaction of colonization and extinction in metapopulations. The role of stochastic variation in demography and marriage pools (and the consequent need for outmarriage in small populations) is also explored in a simulation model.

Chapter 5 considers the implications of contemporary human migration studies for understanding and reconstructing population movements over

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Alan G. Fix
Frontmatter
More information

the longer span of prehistory and human evolution. A major problem is reconciling the range expansions of humans into previously unoccupied regions (the Americas, remote Oceania) with the ethnographic record of mostly local movements. Three examples of suggested large scale colonizations or invasions are presented: the postulated initial spread of *Homo sapiens* from Africa; arguments for and against the spread of agriculture through Europe by Near Eastern migrants; and traditional migratory wave explanations for human diversity in the Malayan Peninsula. All three of these cases demonstrate the great difficulty of discriminating among migration and other causes of genetic distributions. This inherent multicausality reinforces the need for a better understanding of the process of migration and for a general evolutionary theory of its causes and consequences.

Acknowledgments

I would like to thank Gabriel Lasker for suggesting that I write this book and Derek Roberts for his encouraging words on the proposal. Thanks also to Tracey Sanderson at Cambridge University Press for providing further encouragement and helpful advice.

My enormous intellectual debt to the many anthropologists and geneticists who have thought and published on migration will be obvious in the pages that follow. My interpretation of this literature was shaped by my major professor, Frank Livingstone, whose study of the interaction of genetics, ecology, and culture (Livingstone 1958) has always epitomized to me the anthropological approach to human evolution.

The experience of living for over a year with Semai people in Malaysia had a profound effect on my thinking. The adage that fieldwork is crucial to the development of an anthropologist may be old but it is true. I am very grateful to the many Semais who were my teachers in Malaysia. Research in Malaysia was supported by the National Institute of Mental Health and the Wenner Gren Foundation for Anthropological Research.

Sabbatical leave time to complete parts of the text was given by the University of California, Riverside; the Academic Senate of the University also provided financial support through Intramural Research grants.

I would also like to thank Dee Baer, who read and made helpful suggestions on portions of the text, Bryan Epperson for illuminating discussions of spatial modeling in genetics, and Susan Mazur, who provided assistance with the preparation of the manuscript, and Karl Taube, who suggested (and redrew) the cover image of the four god-bearers leaving Aztlan on their epic migration to Tenochtitlán.