

# Genetic Dissection of Complex Traits

Eric S. Lander\* and Nicholas J. Schork

Medical genetics was revolutionized during the 1980s by the application of genetic mapping to locate the genes responsible for simple Mendelian diseases. Most diseases and traits, however, do not follow simple inheritance patterns. Geneticists have thus begun taking up the even greater challenge of the genetic dissection of complex traits. Four major approaches have been developed: linkage analysis, allele-sharing methods, association studies, and polygenic analysis of experimental crosses. This article synthesizes the current state of the genetic dissection of complex traits—describing the methods, limitations, and recent applications to biological problems.

Human genetics has sparked a revolution in medical science on the basis of the seemingly improbable notion that one can systematically discover the genes causing inherited diseases without any prior biological clue as to how they function. The method of genetic mapping, by which one compares the inheritance pattern of a trait with the inheritance patterns of chromosomal regions, allows one to find where a gene is without knowing what it is. The approach is completely generic, being equally applicable to spongiform brain degeneration as to inflammatory bowel disease.

To geneticists, this revolution is really nothing new. Genetic mapping of trait-causing genes to chromosomal locations dates back to the work of Sturtevant in 1913 (1). It has been a mainstay of experimental geneticists who study fruit flies, nematode worms, yeast, and maize and who developed genetic maps containing hundreds of genetic markers that made it possible to follow the inheritance of any chromosomal region in a controlled cross. With the advent of recombinant DNA, genetic mapping was carried to its logical conclusion with the development of positional cloning—the isolation of a gene solely on the basis of its chromosomal location, without regard to its biochemical function. Positional cloning was invented by Bender and colleagues, who used it to isolate the *tithonus* complex in *Drosophila* (2), and it rapidly became a routine technique in flies and worms.

Despite its central role in experimental organisms, genetic mapping hardly figured in the study of humans throughout most of the century. There were two reasons: the lack of an abundant supply of genetic markers with which to study inheritance, and the inability

to arrange human crosses to suit experimental purposes. The key breakthrough was the recognition that naturally occurring DNA sequence variation provided a virtually unlimited supply of genetic markers—an idea first conceived of by Botstein and colleagues for yeast crosses (3) and subsequently for human families (4). With highly polymorphic genetic markers, one could trace inheritance in existing human pedigrees as if one had set up the crosses in the laboratory. These ideas soon led to an explosion of interest in the genetic mapping of rare human diseases having simple Mendelian inheritance. More than 400 such diseases have been genetically mapped in this manner, and nearly 40 have been positionally cloned (5).

Human geneticists are now beginning to explore a new genetic frontier, driven by an inconvenient reality: Most traits of medical relevance do not follow simple Mendelian monogenic inheritance. Such "complex" traits include susceptibilities to heart disease, hypertension, diabetes, cancer, and infection. The genetic dissection of complex traits is attracting many investigators with the promise of shedding light on old problems and is spawning a variety of analytical methods. The emerging issues turn out to be relevant not just to medical genetics, but to fundamental studies of mammalian development and applied work in agricultural improvement. The field is still at an early stage, but it is ready to explode much as it has done in recent years with the analysis of simple traits. The purpose of this article is to synthesize the key challenges and methods, to highlight some enlightening examples, and to identify further needs.

## Complex Traits

The term "complex trait" refers to any phenotype that does not exhibit classic Mendelian recessive or dominant inheritance attributable to a single gene locus. In general, complexities arise when the simple correspondence between genotype and phenotype

breaks down, either because the same genotype can result in different phenotypes (due to the effects of chance, environment, or interactions with other genes) or different genotypes can result in the same phenotype.

To some extent, the category of complex traits is all-inclusive. Even the simplest genetic disease is complex, when looked at closely. Sickle cell anemia is a classic example of a simple Mendelian recessive trait. Yet, individuals carrying identical alleles at the  $\beta$ -globin locus can show markedly different clinical courses, ranging from early childhood mortality to a virtually unrecognized condition at age 50 (6). The trait of severe sickle cell anemia is thus complex, being influenced by multiple genetic factors including a mapped X-linked locus and an inferred autosomal locus that can increase fetal hemoglobin amounts and thereby partially ameliorate the disease (7).

It is often impossible to find a genetic marker that shows perfect cosegregation with a complex trait. The reasons for this can be ascribed to a few basic problems.

**Incomplete penetrance and phenocopy.** Some individuals who inherit a predisposing allele may not manifest the disease (incomplete penetrance), whereas others who inherit no predisposing allele may nonetheless get the disease as a result of environmental or random causes (phenocopy). Thus, the genotype at a given locus may affect the probability of disease, but not fully determine the outcome. The penetrance function  $f(G)$ , specifying the probability of disease for each genotype  $G$ , may also depend on nongenetic factors such as age, sex, environment, and other genes. For example, the risk of breast cancer by ages 40, 55, and 80 is 37%, 66%, and 85% in a woman carrying a mutation at the *BRCA1* locus as compared with 0.4%, 3%, and 8% in a noncarrier (8). In such cases, genetic mapping is hampered by the fact that a predisposing allele may be present in some unaffected individuals or absent in some affected individuals.

**Genetic (or locus) heterogeneity.** Mutations in any one of several genes may result in identical phenotypes, such as when the genes are required for a common biochemical pathway or cellular structure. This poses no problem in experimental organisms, because geneticists can arrange to work with pure-breeding strains and perform crosses to assign mutations to complementation classes. In contrast, medical geneticists typically have no way to know whether two patients suffer from the same disease for

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## **Table of Contents Genetic Dissection Of Complex Traits**

1. Understanding the eBook Genetic Dissection Of Complex Traits
  - The Rise of Digital Reading Genetic Dissection Of Complex Traits
  - Advantages of eBooks Over Traditional Books
2. Identifying Genetic Dissection Of Complex Traits
  - Exploring Different Genres
  - Considering Fiction vs. Non-Fiction
  - Determining Your Reading Goals
3. Choosing the Right eBook Platform
  - Popular eBook Platforms
  - Features to Look for in an Genetic Dissection Of Complex Traits
  - User-Friendly Interface
4. Exploring eBook Recommendations from Genetic Dissection Of Complex Traits
  - Personalized Recommendations
  - Genetic Dissection Of Complex Traits User Reviews and Ratings
  - Genetic Dissection Of Complex Traits and Bestseller Lists
5. Accessing Genetic Dissection Of Complex Traits Free and Paid eBooks

- Genetic Dissection Of Complex Traits Public Domain eBooks
  - Genetic Dissection Of Complex Traits eBook Subscription Services
  - Genetic Dissection Of Complex Traits Budget-Friendly Options
6. Navigating Genetic Dissection Of Complex Traits eBook Formats
    - ePub, PDF, MOBI, and More
    - Genetic Dissection Of Complex Traits Compatibility with Devices
    - Genetic Dissection Of Complex Traits Enhanced eBook Features
  7. Enhancing Your Reading Experience
    - Adjustable Fonts and Text Sizes of Genetic Dissection Of Complex Traits
    - Highlighting and Note-Taking Genetic Dissection Of Complex Traits
    - Interactive Elements Genetic Dissection Of Complex Traits
  8. Staying Engaged with Genetic Dissection Of Complex Traits
    - Joining Online Reading Communities
    - Participating in Virtual Book Clubs
    - Following Authors and Publishers Genetic Dissection Of Complex Traits
  9. Balancing eBooks and Physical Books Genetic Dissection Of Complex Traits
    - Benefits of a Digital Library
    - Creating a Diverse Reading Collection Genetic Dissection Of Complex Traits
  10. Overcoming Reading Challenges
    - Dealing with Digital Eye Strain
    - Minimizing Distractions
    - Managing Screen Time
  11. Cultivating a Reading Routine Genetic Dissection Of Complex Traits
    - Setting Reading Goals Genetic Dissection Of Complex Traits
    - Carving Out Dedicated Reading Time
  12. Sourcing Reliable Information of Genetic Dissection Of Complex Traits
    - Fact-Checking eBook Content of Genetic Dissection Of Complex Traits
    - Distinguishing Credible Sources
  13. Promoting Lifelong Learning
    - Utilizing eBooks for Skill Development

- Exploring Educational eBooks

### 14. Embracing eBook Trends

- Integration of Multimedia Elements
- Interactive and Gamified eBooks

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