



FIGURE 23.13. Fluctuating selection favors recombination only under restrictive conditions. Some kind of frequency-dependent selection must maintain polymorphism by favoring rare alleles. This example shows the **Levene model**, in which juveniles compete within patches with different environments, and the numbers emerging from each patch are fixed (indicated by the sizes of the circles in A–C). (A) Suppose that selection acts on two loci, which determine adaptation to two environmental factors. If there is no correlation between these factors, then there is no epistasis, no linkage disequilibria will be generated, and recombination makes no difference. (B) If there is a consistent correlation between the factors, then there is constant epistasis, and recombination is selected against because it breaks up favorable gene combinations. (C) Recombination can be favored if the correlation between environmental factors *changes* over time, so that epistasis fluctuates. (D) Then positive epistasis (*black*) builds up positive linkage disequilibria (*red*), but by the time these have become strong, epistasis has changed sign, and negative disequilibria are favored. (E) The strength of selection for recombination. Only relative values are shown. With no linkage, all allele frequencies at 1/2, and epistasis fluctuating between 0.1 and –0.1, the average selection against a modifier that reduces recombination by 0.1 is only 0.0000084.