COMMENTARY

A genic view of species integration

L. H. RIESEBERG & J. M. BURKE

Department of Biology, Indiana University, Bloomington, IN, USA

Major botanical advances often suffer the worst of fates – the scientific community ignores them until they are independently 'discovered' or confirmed by zoologists. For example, the principles of inheritance, initially worked out in the garden pea, were not generally accepted until verified in animals (Bateson, 1902). Likewise, the discovery of mobile genetic elements in maize by McClintock (1950) was largely ignored until similar observations were made in bacteria, yeast and flies (Bukhari *et al*., 1977). McClintock (1987) has commented on her disappointment upon receiving only three reprint requests for an important early paper reporting this discovery. More recently, botanical claims for a prominent role for major genes in adaptation (Hilu, 1983; Gottlieb, 1984) were received with scepticism (Coyne & Lande, 1985) until similar findings in animals prompted a re-evaluation (Orr & Coyne, 1992). The 'genic view of speciation' represents another example of a long and widely held view by botanists that is finally being given serious consideration by the zoological community. Obviously, we are gratified to see this occur and thank Chung-I Wu for acknowledging the botanical perspective.

The genic view of speciation in plants had its roots in early observations that plant species often exchange genes without merging (Lotsy, 1925). Groups of species connected by hybridization were termed 'syngameons' (Lotsy, 1925) and became a favourite topic of study by plant evolutionists (Anderson, 1949; Stebbins, 1959; Grant, 1981; Rieseberg, 1997). These observations, combined with evidence for ecologically mediated parapatric speciation (Antonovics, 1968), led botanists to emphasize the role of differential adaptation in the origin and maintenance of species differences (e.g. Clausen, 1951; Macnair *et al*., 1989; Levin, 2000). Selectively maintained species differences must directly or indirectly reduce gene flow (Barton & Hewitt, 1985), and even partial reproductive isolation (RI) may permit divergence at weakly selected loci that otherwise would be homogenized by gene flow.

Although we have highlighted early botanical contributions to this discussion, zoologists have also questioned the requirement for genome-wide isolation. Students of hybrid zones, for example, have long recognized that species boundaries may be semipermeable to introgression (Key, 1968; Barton & Hewitt, 1985), with the movement of alleles dependent on their selection coefficients and linkage relationships. What is perhaps most striking about the Wu review, then, is not its novelty, but rather its derivation from the *Drosophila* speciation community, which until very recently had seemed largely satisfied with the concept of whole genome isolation.

These comments are not intended to minimize the contributions of Wu's review, which represents an important synthesis of many new lines of evidence that call into question the whole genome view of isolation. Of particular interest are data from gene genealogies, which provide compelling evidence both for the mosaic nature of diverging genomes and for the small size of chromosomal segments influenced by isolation genes. Two issues not addressed by Wu, but which have important implications for a genic view of speciation, concern (1) the potential role of factors that modify recombination rates, and (2) the mechanisms that hold species together.

Recombination modifiers

An important consequence of a genic view of speciation is that the allele or chromosomal segment becomes the unit of isolation rather than the entire genome. The effectiveness of an isolation gene is perhaps best measured by the length of the chromosomal segment it protects from gene flow, rather than by its effect on hybrid fitness (Rieseberg, 2001). It is therefore easy to see how recombination modifiers acting to suppress recombination near isolation genes could extend the effects of the latter over much longer chromosomal segments and thereby contribute to species divergence. Chromosomal rearrangements represent one class of recombination modifiers and have been shown in wild sunflower hybrid zones to suppress introgression over much longer chromosomal blocks than isolation genes alone (Rieseberg *et al*., 1999). Genes are also known to affect recombination rates (Sano, 1990), but as far as we are aware, their effects on gene flow and RI have not been studied. Given the very small genomic region (2 kb) influenced by the *Ods* isolation gene in *Drosophila* (Ting *et al*., 2000), studies that investigate the likely synergy between recombination modifiers and isolation genes should be a priority.

Species integration

Wu's review focuses on how species diverge, the major point being that divergence of individual genes rather than entire genomes causes speciation. However, for the study of species divergence to be meaningful, we must first understand how they are held together. We argue that a genic view of species integration solves a three decade-old mystery of how species with little gene flow evolve collectively (Ehrlich & Raven, 1969) and may

Correspondence: L. H. Rieseberg, Department of Biology,
Indiana University, Bloomington, IN 47405, USA.

represent a more revolutionary paradigm shift than the abandonment of the whole genome view of RI.

The traditional view holds that the species evolve as units because of the cohesive effects of gene flow (Mayr, 1963). However, this view was challenged by Ehrlich & Raven (1969), who observed that levels of gene flow in many species are too low to prevent differentiation through drift or local adaptation. There has not been an adequate response to this challenge until very recently (Rieseberg & Burke, 2001). As a result, some evolutionists now consider species to be passive aggregates of evolving units and no different from higher taxa such as genera or families (Mishler, 1999).

Is there any merit to the arguments of Ehrlich & Raven (1969)? We now have a much larger and more accurate body of empirical data to evaluate their claims. In general, genetic estimates of gene flow are higher than those based on field observations (Slatkin, 1987; Ellstrand, 1992). Nonetheless, even these modern estimates indicate that gene flow levels are too low in many taxa to prevent differentiation through drift or local adaptation. Essentially all selfing plants, and more than 50% of amphibians, molluscs, fungi and freshwater fish have N_em values of <1, indicating that differences will accumulate (Ward *et al.*, 1992; Hamrick & Godt, 1996). Even some insect and bird species lack sufficient gene flow to prevent differentiation among populations (e.g. Friesen *et al.*, 1996; Brown *et al.*, 1997).

If levels of gene flow are not high enough to prevent differences from accumulating, then how are species held together? For taxa with very short durations (e.g. asexual microspecies), species integration is probably the result of recent common descent (Grant, 1981). However, sexual species often persist much longer (Stanley, 1978; Levin, 2000) and their integration is not so easily explained. One possibility is to abandon the view that species must remain connected by gene flow across all loci. Perhaps collective evolution of a handful of major genes is enough to account for the apparent integration of species. We propose that it is the dispersal of advantageous alleles that holds most species together (also see Rieseberg & Burke, 2001). Theory indicates that as long as the selective advantage of the new mutant allele is fairly large (s > 0.05), even very low levels of gene flow will enable its efficient spread across the range of a species (Slatkin, 1976; Fig. 1).

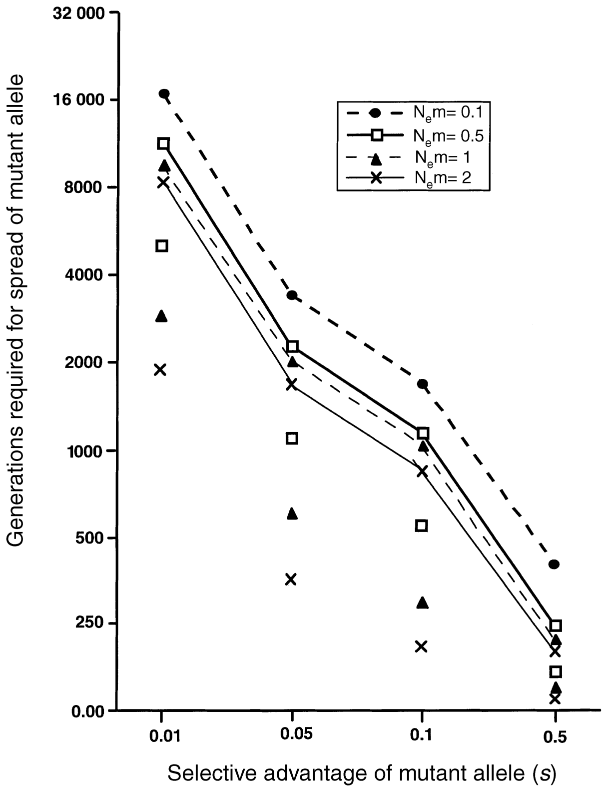

Fig. 1 Number of generations required for a mutant allele to spread across the range of a species (from Rieseberg & Burke, 2001). These calculations are based on a stepping stone model of Slatkin (1976) and assume that 20 steps will be required for the movement of an allele across a species range. Symbols connected by lines show the numbers of generations required for allelic spread in the absence of long-distance dispersal. Symbols without lines indicate the number of generations required for allelic spread with long-distance dispersal. The effects of long-distance dispersal were calculated by assuming that the frequency of migrant individuals reaching a population 20 steps away is 1% of that for reaching an adjacent population (Slatkin, 1976). For $N_em = 0.1$, long-distance dispersal had no impact on rates of spread because long-distance dispersals were so rare as to be nonexistent. All values shown in this figure are extrapolated from Table 1 of Slatkin (1976).

That a genic view of species integration has not been seriously considered in the past is probably because of the widespread acceptance of Fisher's infinitesimal model of adaptive evolution (Fisher, 1930), in which adaptation is assumed to involve many, very small steps. A consequence of this model is that the selective advantage of new mutants must be small, greatly reducing their rate of spread across a subdivided population (Fig. 1). However, the infinitesimal model has been called into question by both empirical (Gottlieb, 1984; Orr, 2001) and theoretical evidence (Orr, 1998). It now appears that discrete traits differentiating taxa often are simply inherited, and that major quantitative trait loci (QTLs) frequently contribute to classic quantitative traits (Orr, 2001). This genetic architecture indicates that a genic view of species cohesion (i.e. collective evolution at a handful of major loci) is plausible, but any conclusions are preliminary because it is not clear whether a mutation with a large phenotypic effect will have an equally large effect on fitness.

Although we do not yet have values of s for any mutation that contributes to fixed differences between species, it is possible to make crude estimates based on what we know about (1) the genetic architecture of a typical trait that differentiates species and (2) selection differentials for both intra- and interspecific trait differences (Rieseberg & Burke, 2001). Calculations for plants reveal that for most traits, *s* for major QTLs is likely to be large enough to facilitate their rapid spread, but that minor QTLs will spread slowly and are unlikely to contribute to the fixed differences between species (see Table 2 of Rieseberg & Burke, 2001). Thus most plant species can be viewed as groups of populations that are evolving collectively at some loci, but likely diverging at others. We are currently compiling QTL magnitudes and selection differentials in animals to see if these arguments can be generalized to a more diverse array of organisms.

One might argue that the complex genetic basis for many of the traits contributing to speciation in *Drosophila* (see Table 1 of Wu, 2001) conflicts with our arguments. This is not necessarily so. First, it is not clear how many of the detected QTLs are fixed between the species. Secondly, the *Drosophila* species studied have higher levels of gene flow and a more continuous population structure than is characteristic of species in many other organismal groups. Thus, the value of *s* required for efficient spread in this system is probably fairly small. Thirdly, the traits listed in Wu's (2001) Table 1 likely represent outcomes of sexual selection, and it seems plausible that even very small phenotypic changes in sexually selected traits may translate into large values of *s*.

Synthesis

In many ways, Wu's genic model for how species diverge is complementary to our genic model of how they are held together. Both minimize the importance of genetic coadaptation and emphasize the importance of individual genes. They also suggest a similar experimental programme that emphasizes the study of individual genes that contribute to fixed differences between species and the intensity of selection required to create these differences. Superficially, we seem to disagree with Wu in our views about the genetics of fixed differences between species, but our apparent disagreement may relate more to the organisms we study (flies vs. plants), and how well they represent the natural world, than to the role of genes in species integration or divergence.

References

Anderson, E. 1949. *Introgressive Hybridization*. John Wiley & Sons, New York.

Antonovics, J. 1968. Evolution in closely adjacent plant populations. VI. Manifold effects of gene flow. *Heredity* **23**: 507–524.

Barton, N.H. & Hewitt, G.M. 1985. Analysis of hybrid zones. *Annu. Rev. Ecol. Syst.* **16**: 113–148.

Bateson, W. 1902. *Mendel's Principles of Heredity: A Defense*. University Press, Cambridge, MA.

Brown, J.M., Leebens-Mack, H.H., Thompson, J.N., Pellmyr, O. & Harrison, R.G. 1997. Phylogeography and host association in a pollinating seed parasite *Greya politella* (Lepidoptera: Prodoxidae). *Mol. Ecol.* **6**: 215–224.

Bukhari, A.I., Shapiro, J.A. & Adhya, S.L. (eds) 1977. *DNA Insertion Elements, Plasmids, and Episomes*. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY.

Clausen, J. 1951. *Stages in the Evolution of Plant Species*. Cornell University Press, Ithaca, NY.

Coyne, J.A. & Lande, R. 1985. The genetic basis of species differences in plants. *Am. Nat.* **126**: 141–145.

Ehrlich, P.R. & Raven, P.H. 1969. Differentiation of populations. *Science* **165**: 1228–1232.

Ellstrand, N.C. 1992. Gene flow among seed plant populations. *New For.* **6**: 241–256.

Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.

Friesen, V.L., Montevecchi, W.A., Baker, A.J., Barrett, R.T. & Davidson, W.S. 1996. Population differentation and evolution in the common guillemot *Uria aalge*. *Mol. Ecol.* **5**: 793–805.

Gottlieb, L.D. 1984. Genetics and morphological evolution in plants. *Am. Nat.* **123**: 681–709.

Grant, V. 1981. *Plant Speciation*. Columbia University Press, New York.

Hamrick, J.L. & Godt, M.J.W. 1996. Effects of life history traits on genetic diversity in plant species. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* **351**: 1291–1298.

Hilu, K.W. 1983. The role of single-gene mutations in the evolution of flowering plants. *Evol. Biol.* **26**: 97–128.

Key, K.H.L. 1968. The concept of stasipatric speciation. *Syst. Zool.* **17**: 14–22.

Levin, D.A. 2000. *The Origin, Expansion, and Demise of Plant Species*. Oxford University Press, New York.

Lotsy, J.P. 1925. Species or Linneon? *Genetica* **7**: 487–506.

Macnair, M.R., Macnair, V.E. & Martin, B.E. 1989. Adaptive speciation in *Mimulus* – an ecological comparison of *Mimulus cupriphilus* with its presumed progenitor, *Mimulus guttatus. New Phytol.* **112**: 269–279.

Mayr, E. 1963. *Animal Species and Evolution*. Belknap Press, Cambridge, MA.

McClintock, B. 1950. The origin and behavior of mutable load in maize. *Proc. Natl. Acad. Sci. USA* **36**: 344–355.

McClintock, B. 1987. *The Discovery and Characterization of Transposable Elements in Maize*. Garland Publishing, New York.

Mishler, B.D. 1999. Getting rid of species. In: *Species: New Interdisciplinary Essays* (R. A. Wilson, ed.), pp. 307–316. MIT Press, Cambridge, MA.

Orr, A. 1998. The population genetics of adaptation: the distribution of factors fixed during adaptive evolution. *Evolution* **52**: 935–949.

Orr, H.A. 2001. The genetics of species differences. *TREE* **16**: 343–350.

Orr, H.A. & Coyne, J.A. 1992. The genetics of adaptation – a reassessment. *Am. Nat.* **140**: 725–742.

Rieseberg, L.H. 1997. Hybrid origins of plant species. *Annu. Rev. Ecol. Syst.* **28**: 359–389.

Rieseberg, L.H. 2001. Chromosomal rearrangements and speciation. *TREE* **16**: 351–358.

Rieseberg, L.H. & Burke, J.M. 2001. The biological reality of species: gene flow, selection, and collective evolution. *Taxon* **50**: 47–67.

Rieseberg, L.H., Whitton, J. & Gardner, K. 1999. Hybrid zones and the genetic architecture of a barrier to gene flow between two sunflower species. *Genetics* **152**: 713–727.

Sano, Y. 1990. The genetic nature of gametic eliminator in rice. *Genetics* **125**: 183–191.

Slatkin, M. 1976. The rate of spread of an advantageous allele in a subdivided population. In: *Population Genetics and Ecology* (S. Karlin & E. Nevo, eds), pp. 767–780. Academic Press, New York.

Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. *Science* **236**: 787–792.

Stanley, S.M. 1978. Chronospecies' longevities, the origin of genera, and the punctuational model of evolution. *Paleobiology* **4**: 26–40.

Stebbins, G.L. 1959. The role of hybridization in evolution. *Proc. Am. Phil. Soc.* **103**: 231–251.

Ting, C.T., Tsaur, S.C. & Wu, C-I. 2000. The phylogeny of closely related species as revealed by the genealogy of a speciation gene, *Odysseus*. *Proc. Natl. Acad. Sci. USA* **97**: 5313–5316.

Ward, R.D., Skibinski, D.O.F. & Woodwark, M. 1992. Protein heterozygosity, protein-structure, and taxonomic differentiation. *Evol. Biol.* **26**: 73–159.

Wu, C-I. 2001. The genic view of the process of speciation. *J. Evol. Biol.* **14**: 851–865.