

## Is population genetics mired in the past?

In a recent *TREE* perspective, Bossart and Prowell<sup>1</sup> concluded that researchers estimating population structure used antiquated methods, and failed to acknowledge and test underlying model assumptions. We found these conclusions surprisingly pessimistic and decided to examine 67 papers on population structure from *Evolution* and *Molecular Ecology* (1997). Although many studies in *Evolution* were based solely on allozymes (12/25), this was true of only 1/28 papers in *Molecular Ecology*. The journal bias might explain some of Bossart and Prowell's findings, because they reviewed papers in *Evolution* that tended to focus primarily on theoretical problems in evolution, and only secondarily on estimating population structure.

We found neither that 'cautions [regarding analyses of population structure] have not been widely embraced by the scientific community', nor that 'conclusions often are drawn ... even though there are multiple, equally viable interpretations'<sup>1</sup>. Only 14/67 papers calculated  $Nm$  (gene flow) and only two interpreted  $Nm$  literally. Most researchers viewed their results from a number of perspectives (e.g. historical association versus contemporary gene flow), and it was nearly impossible to find studies that did not use multiple loci and conduct sensitivity analyses over loci and/or populations.

Departures from equilibrium undoubtedly bias gene flow estimates in many cases. However, we disagree that allozymes yield no useful information regarding the movement of individuals. How can we test this assertion? Bossart and Prowell stated that comparisons with direct estimates of dispersal are 'the only valid approach to the study and interpretation of gene flow in an ecological context'. We had difficulty interpreting this statement because it is well known that dispersal and gene flow are not equivalent for many reasons, and that rare dispersal events overlooked in most ecological studies can heavily influence indirect gene flow estimates<sup>2,3</sup>.

Furthermore, there are other valid approaches for appraising gene flow estimates, such as examining correlations between  $F_{st}$  and morphological indicators of dispersal ability. It has been repeatedly shown that larval time is correlated with population differentiation in marine invertebrates<sup>4,5</sup> and vertebrates<sup>6</sup>, flightless insects tend to have higher values of  $F_{st}$  than flight-form insects<sup>7-11</sup>, and  $F_{st}$  values in plants are related to mode of seed dispersal<sup>12</sup>. These are not isolated examples; three separate reviews have found that wide dispersers tend to have higher estimates of  $Nm$  and lower estimates of  $F_{st}$  than those with restricted dispersal<sup>13-15</sup>. If ongoing gene flow has a negligible impact on allozyme differentiation among populations, there should be no correlation between population genetic differentiation and any measure of dispersal ability.

To conclude that population genetics is 'no longer advancing [because of] our reliance on easy to apply, conventional indirect methods' implies that: (1) most evolutionary biologists use allozymes and  $F$ -statistics, and (2) this has stagnated the field. Yet the exclusive use of allozymes is becoming rarer and new statistical

methodologies are published almost monthly. Therefore, we take a less pessimistic view than Bossart and Prowell. We believe that the limitations of traditional approaches are generally understood and that they still provide a valuable first approximation in many cases. Methods for determining the relative contributions of history and current gene flow are already being developed and utilized. Judging from the recent literature, we would argue that advancement, not stagnation, is the current state of the field.

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## Reply from J.L. Bossart and D. Pashley Prowell

We thank Bohonak *et al.* for the opportunity to expand upon our perspective of gene flow estimates<sup>1</sup>. We are comfortable with our portrayal of the state of this field based on data from *Evolution*. *Evolution* was selected because it has a long history as a top journal focusing on empirically based population genetics, has a vast readership and high citation rates. *Molecular Ecology*, however, is a new, more specialized and less available journal.

We agree that most indirect studies of gene flow report data for multiple loci and many use resampling techniques or regression to conduct sensitivity analyses. The issue is whether these

are informative comparisons. For example, have estimates averaged over loci advanced our understanding of gene frequency evolution when estimates among loci vary, not uncommonly, by orders of magnitude?<sup>2?</sup>

Our perspective acknowledged problems associated with direct measures of dispersal. Like others<sup>3</sup>, however, we emphasized the essential information these estimates provide. Correlational approaches between  $F_{st}$  and life history traits to assess accuracy of genetic methods, as advocated by Bohonak *et al.*, are statistically weak and confounded by evolutionary history – for example, higher  $F_{st}$  values in sessile versus vagile organisms may reflect vicariant events.

Application of conventional indirect methods to address ecological questions is inappropriate for two reasons. First, there is no temporal reference point. Do data reveal processes operating over ten years, 100 years, 1000 years or 10 000 years? Second,  $Nm$  changes only trivially between  $Nm = 2$  and  $Nm = \text{infinity}$ , so  $Nm = 2$  is virtually indistinguishable from  $Nm = 2000$  (Ref. 2). Thus, conventional approaches have insufficient power to address relative rates of gene flow among populations impinged upon by human activities, metapopulation dynamics, trophic interactions or relative magnitude of gene flow versus selection.

Our overall conclusion that indirect methods 'provide a useful starting point'<sup>1</sup> was mirrored by Bohonak *et al.* in their statement that indirect methods 'provide a valuable first approximation'. We part company, however, on the widespread use of new analytical models, as our review validated. As this changes, the field will advance.

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