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Circuit theory predicts gene flow in plant and animal populations

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Maintaining connectivity for broad-scale ecological processes like dispersal and gene flow is essential for conserving endangered species in fragmented landscapes. However, determining which habitats should be set aside to promote connectivity has been difficult because existing models cannot incorporate effects of multiple pathways linking populations. Here, we test an ecological connectivity model that overcomes this obstacle by borrowing from electrical circuit theory. The model vastly improves gene flow predictions because it simultaneously integrates all possible pathways connecting populations. When applied to data from threatened mammal and tree species, the model consistently outperformed conventional gene flow models, revealing that barriers were less important in structuring populations than previously thought. Circuit theory now provides the best-justified method to bridge landscape and genetic data, and holds much promise in ecology, evolution, and conservation planning.

Gulo gulo | isolation by resistance | landscape connectivity | *Swietenia macrophylla* | landscape genetics

Preserving and restoring connectivity for broad-scale ecological processes, such as dispersal and gene flow, has become a major conservation priority (1, 2). Conservation organizations are investing considerable resources—and asking governments to do the same—to set aside land to promote connectivity (3). A major impediment to this goal is the difficulty in predicting how different land use, climate change, or reserve design scenarios will affect connectivity, and conservation planning decisions are often made without quantifying benefits for the ecological processes they are meant to conserve. If scarce conservation dollars are to be spent effectively, conservation biologists need clear, efficient, and reliable tools relating landscape composition and pattern to important ecological processes (4).

Gene flow is a critical ecological process with conservation benefits ranging from promoting the persistence of small populations to spreading adaptive traits in changing environments (5–8). Because of these important ecological and evolutionary roles, a new and rapidly growing field—landscape genetics—is primarily dedicated to understanding and predicting how landscape characteristics affect gene flow (5). By combining genetic, computational, and spatial analytic tools unavailable a decade ago, the interdisciplinary field has yielded insights relevant not only to conservation (e.g., refs. 8 and 9), but to fields such as evolution (10), infectious disease ecology (11), and population ecology (12).

Yet progress in all of these fields has been hampered by a lack of models capable of predicting gene flow from landscape structure. As a result, typical landscape genetic analyses simply detect genetic discontinuities and propose ad hoc explanations based on coincident landscape features, rather than testing *a priori* predictions of how such features are expected to influence genetic structure. This hinders hypothesis testing and leaves conservation planners without validated metrics of how landscape change will affect genetic connectivity. Although a growing number of studies are incorporating landscape data into genetic predictions and conservation plans using least-cost path

(LCP) modeling (9, 13–16), gene flow among real populations is not restricted to single, optimal pathways, as LCP models assume; rather, it occurs over multiple pathways and often involves indirect allele movements spanning many generations (17). Thus, to support conservation planning and to enable hypothesis testing in landscape genetics, theoretically justified models of how landscape features facilitate or impede gene flow over multiple, direct and indirect pathways are needed.

Here, we use electrical circuit theory to overcome these limitations and test its performance using data from threatened plant and animal species. The isolation-by-resistance (IBR) model improves over previous gene flow models by using the resistance distance, a graph-theoretic distance metric based in circuit theory (18), to simultaneously consider all possible pathways connecting population pairs (19). The analogy between electrical and genetic connectivity is simple: as multiple or wider conductors connecting two electrical nodes allow greater current flow than would a single, narrow conductor, multiple or wider habitat swaths connecting populations allow greater gene flow. The model is further grounded in rigorous connections between effective resistances in electrical networks and gene coalescence times in population networks (19), giving it a stronger theoretical foundation than either conventional isolation-by-distance (IBD) models (17, 20) or popular LCP models. The IBR model has been shown to reliably predict the effects of landscape heterogeneity on gene flow and genetic structure in artificial population networks (19) but has thus far not been tested with real landscape or genetic data.

Results

To test the IBR model, we used landscape and genetic data from two threatened species. Both are vulnerable to extinction because of habitat loss and overexploitation (21), and conservation efforts rely on our ability to identify important landscape connections and barriers. The plant data set consisted of eight Central American populations of big-leaf mahogany (*Swietenia macrophylla*), an insect-pollinated tropical tree, with 287 individuals typed at seven microsatellite loci by Novick *et al.* (22) (Fig. 1A). The animal data set consisted of 12 western north American populations of the wolverine (*Gulo gulo*), a large circumpolar mustelid, with 461 animals typed at 12 microsatellite loci by Kyle and Strobeck (23) (Fig. 1B). These previous studies had used conventional IBD analyses to draw conclusions regarding the evolutionary history and future conservation needs of the species. However, such analyses assume habitat to be unbounded and were unable to incorporate effects of spatial heterogeneity, such as range limits, into predictions of genetic differentiation.

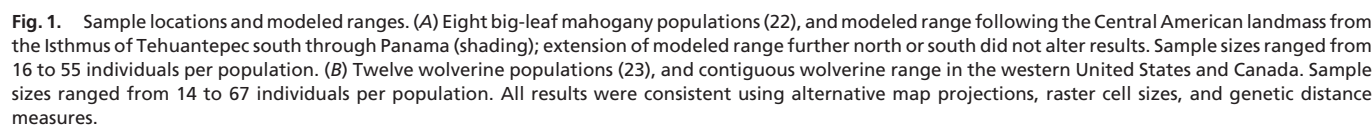
Author contributions: B.H.M. and P.B. designed research; B.H.M. performed research; B.H.M. contributed new reagents/analytic tools; B.H.M. analyzed data; and B.H.M. and P.B. wrote the paper.

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Barrier Effects. Incorporating range shape using circuit theory not only improved gene flow predictions, but also illuminated the effects of other important factors driving population structure. Both of the original studies had found residual variation unexplained by distance and had attributed that variation to migration barriers or other factors driving differentiation within each species' range. For example, Novick *et al.* (22) noted that the southernmost mahogany population [Tonosí (Fig. 1A)] appeared to be more differentiated from other populations than would be expected from distance alone, and speculated that the increased differentiation may result from geographic barriers and/or historical events. We confirmed that the population was more differentiated than expected from either its distance [$r = 0.82$, $P = 0.0002$ (Fig. 2A)] or log-transformed distance [$r = 0.87$,

Three main results from our analyses have relevance for landscape genetics and for conservation. First, circuit theory consistently outperformed competing models for both the plant and animal data sets. Combined with its stronger theoretical foun-

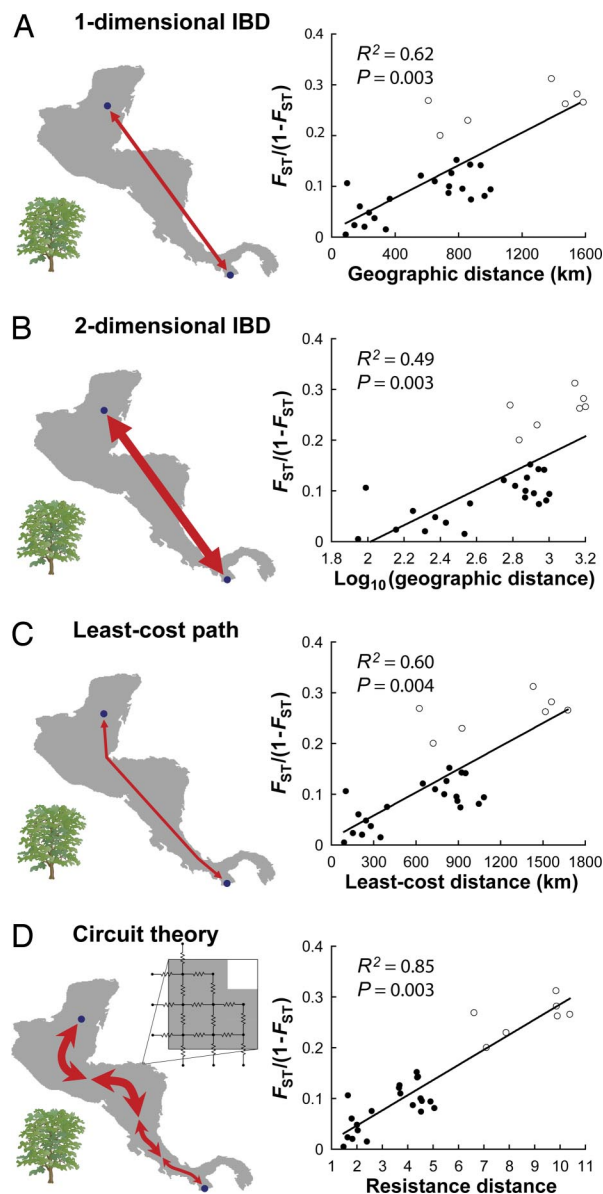


Fig. 2. Circuit theory outperforms standard models of genetic differentiation among mahogany populations. Range maps illustrate how pairwise isolation is measured under the competing models between two example populations (Nuevo Becal and Tonosí), and scatterplots show performance of the models for all population pairs. Models compared are one-dimensional IBD (A), which assumes habitat to be arranged in an infinite linear array; two-dimensional IBD (B), which assumes habitat to be arranged in an infinite plane; LCP (C), which incorporates spatial heterogeneity but assumes differentiation to vary with distance measured along a single, optimal path; and IBR (D), which predicts greater gene flow and less genetic differentiation with multiple pathways and wider habitat swaths connecting populations. (D Inset) Habitat modeled as a conductive surface. Open circles indicate pairwise comparisons including Tonosí; filled circles indicate pairwise comparisons among the remaining seven populations. Linear regression lines include all populations.

dation and better performance with simulated landscape and genetic data (19), this real-world validation means that IBR is better justified for use in landscape genetics and conservation planning than commonly applied IBD or LCP models. Second, we found that range shape—a factor rarely considered in landscape genetic studies—can dramatically affect genetic structure. Thus, applying models that ignore range shape could distort genetic data analyses or predictions of how landscape change will

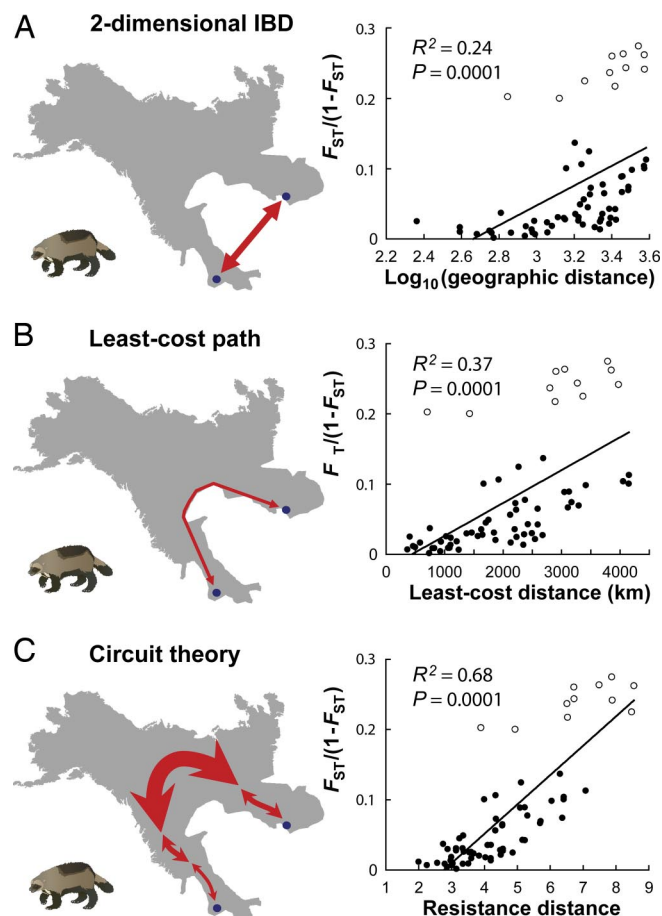


Fig. 3. Circuit theory outperforms standard models of genetic differentiation among wolverine populations. Range maps illustrate how pairwise isolation is measured under the competing models between two example wolverine populations (Idaho and Manitoba). Models compared are two-dimensional IBD (A), the better justified IBD model (see *IBD Predictions* under *Methods*), LCP (B), and IBR (C). Open circles indicate pairwise comparisons including Idaho. Linear regression lines include all populations.

affect genetic connectivity. Finally, much of landscape genetics is concerned with detecting barriers (5), but conventional analyses may exaggerate their effects. In both of the cases we examined, traditional tests for barrier effects could only demonstrate that something other than geographic distance was at work, where “something” might simply reflect nuisance factors like oceans or range limits. By correcting for range shape, the IBR model allowed stronger inference about genuine impediments to gene flow.

Circuit theory gives a better picture of gene flow in these landscapes for several reasons. Unlike IBD models (Fig. 2A and B and Fig. 3A), IBR explicitly incorporates effects of limited and irregular habitat extent, and obviates the need to choose between one- and two-dimensional habitat models. Unlike LCP models (Figs. 2C and 3B), IBR also accounts for multiple pathways and wider habitat swaths connecting populations (Figs. 2D and 3C). Such features strongly affect patterns of genetic differentiation by increasing migration rates, decreasing rates of genetic drift, and lengthening within-population coalescence times relative to between-population coalescence times (17, 19). For the mahogany data, IBR correctly predicted greater gene flow in the north, where habitat is broadly distributed (and more potential pathways exist), and less in the south, where habitat becomes more constricted. By contrast, within-habitat LCP

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