



Circuit-theory applications to connectivity science and conservation

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Abstract: *Conservation practitioners have long recognized ecological connectivity as a global priority for preserving biodiversity and ecosystem function. In the early years of conservation science, ecologists extended principles of island biogeography to assess connectivity based on source patch proximity and other metrics derived from binary maps of habitat. From 2006 to 2008, the late Brad McRae introduced circuit theory as an alternative approach to model gene flow and the dispersal or movement routes of organisms. He posited concepts and metrics from electrical circuit theory as a robust way to quantify movement across multiple possible paths in a landscape, not just a single least-cost path or corridor. Circuit theory offers many theoretical, conceptual, and practical linkages to conservation science. We reviewed 459 recent studies citing circuit theory or the open-source software Circuitscape. We focused on applications of circuit theory to the science and practice of connectivity conservation, including topics in landscape and population genetics, movement and dispersal paths of organisms, anthropogenic barriers to connectivity, fire behavior, water flow, and ecosystem services. Circuit theory is likely to have an effect on conservation science and practitioners through improved insights into landscape dynamics, animal movement, and habitat-use studies and through the development of new software tools for data analysis and visualization. The influence of circuit theory on conservation comes from the theoretical basis and elegance of the approach and the powerful collaborations and active user community that have emerged. Circuit theory provides a springboard for ecological understanding and will remain an important conservation tool for researchers and practitioners around the globe.*

Keywords: barriers, corridors, dispersal, ecological flow, electrical current, landscape genetics

Aplicaciones de la Teoría de Circuitos a la Conservación y a la Ciencia de la Conectividad

Resumen: *Quienes practican la conservación han reconocido durante mucho tiempo que la conectividad ecológica es una prioridad mundial para la preservación de la biodiversidad y el funcionamiento del*

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ecosistema. Durante los primeros años de la ciencia de la conservación los ecólogos difundieron los principios de la biografía de islas para evaluar la conectividad con base en la proximidad entre el origen y el fragmento, así como otras medidas derivadas de los mapas binarios de los hábitats. Entre 2006 y 2008 el fallecido Brad McRae introdujo la teoría de circuitos como una estrategia alternativa para modelar el flujo génico y la dispersión o las rutas de movimiento de los organismos. McRae propuso conceptos y medidas de la teoría de circuitos eléctricos como una manera robusta para cuantificar el movimiento a lo largo de múltiples caminos posibles en un paisaje, no solamente a lo largo de un camino o corredor de menor costo. La teoría de circuitos ofrece muchos enlaces teóricos, conceptuales y prácticos con la ciencia de la conservación. Revisamos 459 estudios recientes que citan la teoría de circuitos o el software de fuente abierta Circuitscape. Nos enfocamos en las aplicaciones de la teoría de circuitos a la ciencia y a la práctica de la conservación de la conectividad, incluyendo temas como la genética poblacional y del paisaje, movimiento y caminos de dispersión de los organismos, barreras antropogénicas de la conectividad, comportamiento ante incendios, flujo del agua, y servicios ambientales. La teoría de circuitos probablemente tenga un efecto sobre la ciencia de la conservación y quienes la practican por medio de una percepción mejorada de las dinámicas del paisaje, el movimiento animal, y los estudios de uso de hábitat, y por medio del desarrollo de nuevas herramientas de software para el análisis de datos y su visualización. La influencia de la teoría de circuitos sobre la conservación viene de la base teórica y la elegancia de la estrategia y de las colaboraciones fuertes y la comunidad activa de usuarios que han surgido recientemente. La teoría de circuitos proporciona un trampolín para el entendimiento ecológico y seguirá siendo una importante herramienta de conservación para los investigadores y practicantes en todo el mundo.

Palabras Clave: barreras, corredores, corriente eléctrica, dispersión, flujo ecológico, genética del paisaje

摘要: 保护实践者长期以来一直将生态连接度视为保护生物多样性和生态系统功能的当务之急。在保护科学发展早期,生态学家将岛屿生物地理学的原理进行扩展,基于源斑块邻近度和其它来自二元生境图的指标来评估连接度。2006年到2008年,已故的Brad McRae引入了电路理论,作为模拟基因流和生物体扩散或移动路径的新方法。他用电路理论中的概念和指标开发了一种稳健的方法来量化景观中多种可能的移动路径,而这不只是一条最低成本的路径或廊道。电路理论为保护科学提供了许多理论、概念和实践方面的联系。我们综述了近期引用电路理论或是开源软件Circuitscape的459项研究,重点关注电路理论在连接度保护科学与实践中的应用,包括景观和种群遗传学、生物体运动和扩散路径、连接度的人为障碍、火灾、水流和生态系统服务等问题。电路理论通过帮助理解景观动力学、动物移动和生境利用研究,以及开发新的数据分析和可视化软件工具,影响着保护科学和实践者。电路理论对保护的影响来自于该方法的理论基础和优雅性,以及现已出现的强大的合作队伍和活跃的用户群体。电路理论为生态学理解提供了跳板,并将继续作为全球研究人员和实践者的重要保护工具。翻译:胡怡思;审校:聂永刚

关键词: 障碍,廊道,扩散,生态流,电路模型,景观

Introduction

Ecological connectivity is a global priority for preserving biodiversity and ecosystem function (UNEP 2015; IUCN 2017) and has long been of interest to conservation scientists (Harris 1984). In the early years of conservation science, ecologists extended principles of island biogeography to assess connectivity based on proximity to source patches (MacArthur & Wilson 1967) and other metrics derivable from binary maps containing habitat patches embedded in a nonhabitat matrix (e.g., With et al. 1997). The introduction of least-cost modeling in the early 1990s (Knaapen et al. 1992) was a major advancement in connectivity and movement corridor research and quickly became the dominant paradigm for evaluating connectivity for animals. However, least-cost paths often have clear limitations, including an assumption that individuals have perfect knowledge of the landscape and therefore select a single optimal route.

In 3 papers published from 2006 to 2008, Brad McRae introduced circuit theory to many ecologists and conservation scientists as an alternative, process-driven approach to modeling gene flow and the dispersal or movement routes of organisms (see below). Drawing from his background in electrical engineering, as well as the seminal work of Doyle and Snell (1984) and others, McRae's key innovation was recognizing that circuit theory permitted a robust way to quantify gene flow. The approach provided a much-needed theoretical basis for understanding and mapping patterns of connectivity and has been rapidly adopted in conservation science, other ecological disciplines, and beyond. The development of accompanying software, such as the open-source program Circuitscape (McRae et al. 2008, 2013; www.circuitscape.org), has provided accessible means of implementing circuit theory concepts across a range of projects and disciplines. Additional software and development topics are described in Supporting Information.

In the wake of Brad McRae's untimely death in July 2017 (Lawler et al. 2018), we explored the importance and key contributions of circuit theory to connectivity conservation and related issues. We considered the foundations of circuit theory, including key concepts, outputs, and comparisons with other approaches to evaluating connectivity and the theory's diversity of applications in conservation and ecology, including a synthesis of relevant publications across a variety of topics and from multiple geographies. Finally, we considered how new applications of circuit theory might continue to benefit conservation theory and practice, particularly in an era of global change.

Foundations of Circuit Theory in Conservation

Brad McRae posited circuit theory as an elegant alternative approach to model gene flow and organismal movement in a series of 3 papers published during 2006–2008. McRae (2006) linked the findings of Doyle and Snell (1984) and Chandra et al. (1996) to population genetics and landscape ecology. Specifically, Doyle and Snell (1984) demonstrated that resistance distances from circuit theory are directly proportional to the movements of Markovian random walkers on graphs, and Chandra et al. (1996) related resistance distances to “commute times,” or the time it takes a random walker to travel from one point to another and back again. McRae (2006) described the concept that the genetic distance among subpopulations of interest can be estimated by representing the landscape as a circuit board, where each pixel in a raster depiction of the landscape is a resistor, and gene flow between any 2 subpopulations occurs via all possible chains of resistors linking them, not just along the single chain with the lowest sum of resistances (i.e., the least-cost path). He coined this notion “isolation by resistance” (IBR), which has practical consequences in the context of conservation. For example, in IBR (but not least-cost models) increasing the number of paths always decreases the total resistance and genetic distance among subpopulations, and habitat degradation increases genetic distance, even outside the least-cost path. Its theoretical foundation and computational efficiency has made circuit theory a powerful and defensible tool for understanding potential gene flow, animal movement routes, and landscape connectivity.

The second foundational paper (McRae & Beier 2007) demonstrated that IBR explained genetic patterns of mammal (wolverine [*Gulo gulo*]) and plant (bigleaf mahogany [*Swietenia macrophylla*]) populations about 50–200% better than 2 conventional approaches, namely isolation by distance and least-cost paths. The findings were striking because the species were undergoing rapid human-caused demographic changes, violating the IBR model assumption that all populations are in genetic equilibrium (i.e., based on the response variable, F_{ST}).

This robustness suggested that circuit theory could be applied to the variety of other landscapes experiencing human-caused changes.

Finally, McRae et al. (2008) introduced many readers to the key concepts and metrics used in electrical circuit theory and how they could be applied to model and map the process of connectivity over extensive landscape, habitat, or population networks (based on georeferenced raster grids). Two of the most commonly used metrics include current density and effective resistance. Current density provides an estimate of the net movement probabilities (or flow) of random walkers through a given grid cell. Effective resistance permits a pairwise distance-based measure of isolation among populations or sites (McRae & Beier 2007). McRae et al. (2008) illustrated how circuit theory could be used to identify multiple (i.e., redundant) movement pathways or habitat corridors and reveal, for example, critical pinch points that constrain potential flow between focal areas. Redundancy is a measure of the number of possible pathways between focal points and reflects a fundamental relationship that is the ratio of least-cost distance to effective resistance (see Koen et al. [2012] and Marrotte and Bowman [2017] for in-depth treatments of this topic). Because circuit theory uses the same underlying landscape resistance data used by least-cost and other connectivity models, it could readily be added to the toolkits of conservation planners. In addition, McRae et al. (2008) introduced many readers to Circuitscape software, opening the door to diverse applications.

Applications of Circuit Theory to Conservation

Circuit theory has been applied to a wide range of conservation questions and challenges. Because Circuitscape is the principal tool that researchers and practitioners use to apply the method, we reviewed 459 papers identified through either a Web of Science or Google Scholar search of work that cited McRae et al. (2008) or the Circuitscape user guide (McRae & Shah 2009; McRae et al. 2013). Of these studies, 277 directly used the software. Applications ranged across disciplines from conservation to evolutionary biology, from anthropology to epidemiology, and more. Circuitscape has been applied on every continent (including off the coast of Antarctica [Dambach et al. 2016]), and several applications spanned multiple continents (e.g., Lawler et al. 2013; Tassi et al. 2015) (Fig. 1). Whatever the geographic or conservation context, Circuitscape has been most frequently applied to single, focal species, though studies of 2 or more species are becoming more common (Fig. 2). The vast majority of studies addressed animals ($n = 228$), but 10 focused on plants and 1 on protists (Dong et al. 2016). Mammals were by far the most common vertebrates studied, followed by birds, amphibians, reptiles, and fish, though arthropods have been studied almost as frequently as birds (Fig. 3).

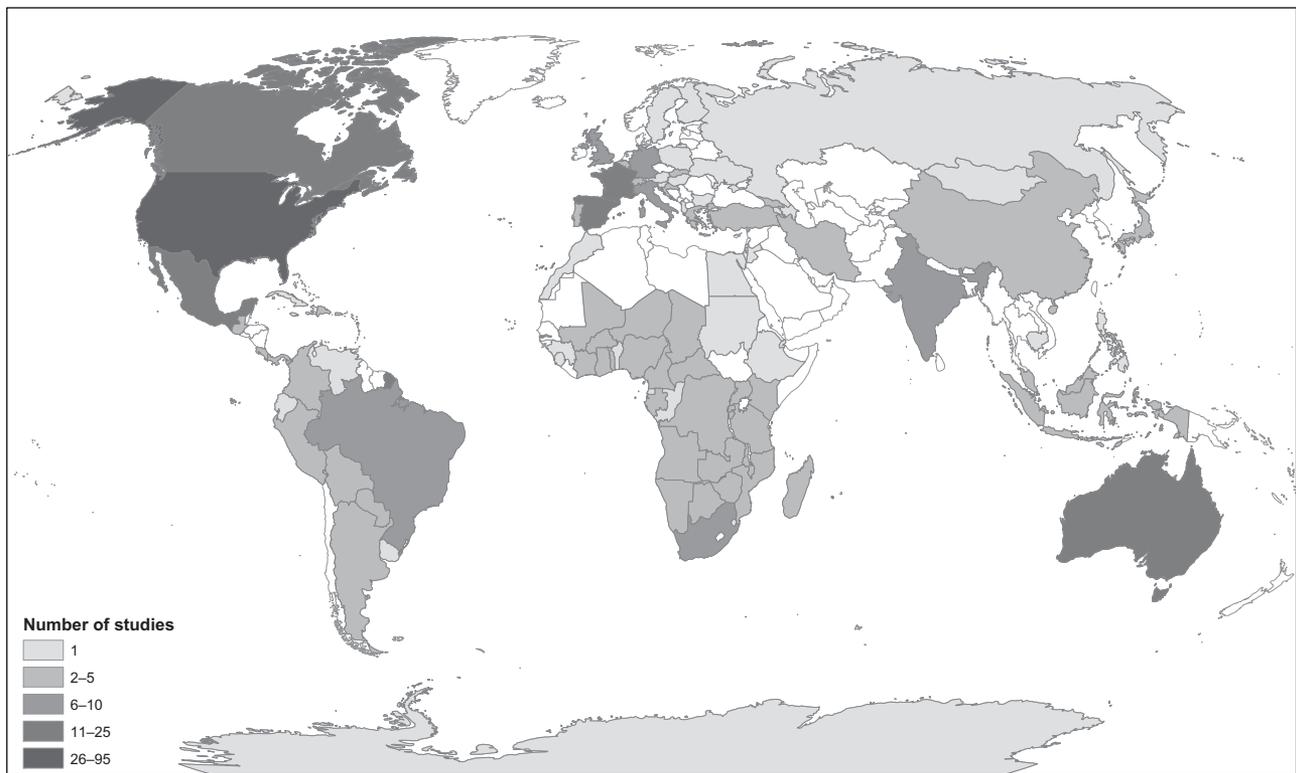


Figure 1. Number of peer-reviewed studies that used Circuitscape by nation from January 2009 to February 2018. Three studies that were continental in their spatial extent are not represented.

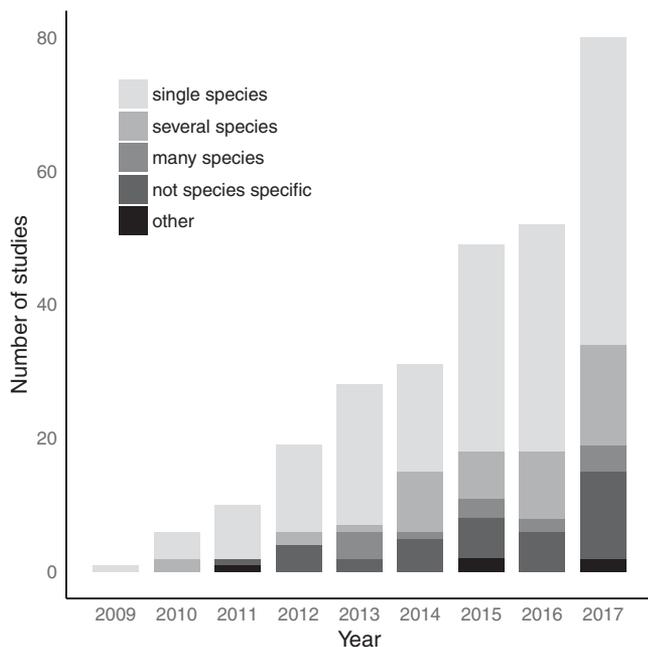


Figure 2. Number of peer-reviewed studies of 5 types that used Circuitscape from 2009 to 2017 (several species, 2–10; many species, >10; not species specific, specific species not targeted; other, models compared or physical processes modeled [e.g., hydraulic resistance in roots [Zeppenfeld et al. 2017]).

At least 5 mammal-focused studies addressed human genomics or movement patterns.

We examined the impressive range and diversity of circuit-theoretic and Circuitscape applications and considered how circuit theory has been used to understand landscape and population genetics, the movement and dispersal paths of organisms, anthropogenic barriers to connectivity, fire behavior, water flow, and ecosystem services. Additional topic areas and examples are given in Supporting Information.

Landscape and Population Genetics

The foundational papers on circuit theory energized the emerging field of landscape genetics (Guillot et al. 2009; Manel & Holderegger 2013). Use of genetic data to inform models of landscape resistance to movement with circuit theory has since become standard practice (Zeller et al. 2012; Simpkins et al. 2018). This information has been useful in formalizing the incorporation of landscape structure and complexity into conservation plans for many species and ecosystems. For example, the multispecies Washington Connected Landscapes project (WWHCWG 2010) incorporated mountain goat (*Oreamnos americanus*) connectivity based on genetic circuit-theory models (Shirk et al. 2010), and the Washington-British Columbia Climate-Connectivity project (Krosby

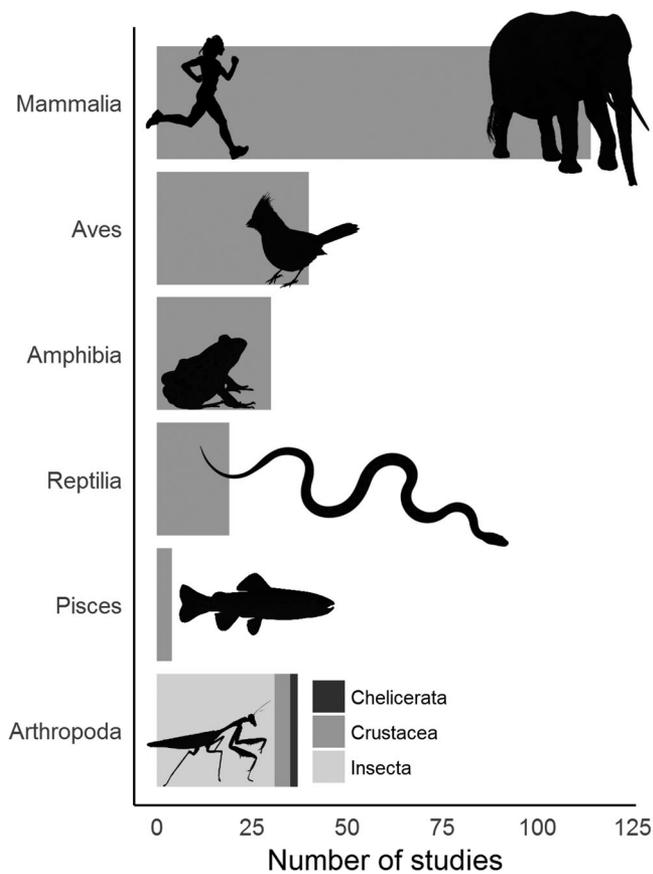


Figure 3. Number of peer-reviewed studies that applied *Circuitscape* to research questions in the animal kingdom from January 2009 to February 2018.

et al. 2016) spurred additional research based on genetic and circuit theoretic approaches for assessing potential impacts and adaptation actions under climate change (Parks et al. 2015). Circuit theory has been used in multiple ways to explore the potential impacts of climate change on landscape genetics. A few studies explored how historical changes to Earth's climate have affected connectivity, resulting in modern genetic patterns (Bell et al. 2010; Ortego et al. 2015), or have examined the impact climate change will have on future genetic patterns (Velo-Anton et al. 2013).

Despite its widespread use and contributions, the application of circuit theory in genetics is not yet fully realized. Initial statistical approaches based on comparing interindividual genetic distances with resistance distances (e.g., with Mantel tests) often led to faulty inferences by incorrectly assuming linearity, ignoring spatial structure in the data, and failing to recognize that genetic distances can be affected by variable local population density (Legendre & Fortin 2010; Jaquière et al. 2011; Graves et al. 2013). Other recent approaches use appropriate probability distributions for distance data (Hanks &

Hooten 2013) and newer IBR models accommodate variation in population sizes to some extent (Petkova et al. 2016). Even if the basic IBR model assumptions are met, challenges remain in automating procedures for how to weigh various environmental factors and how to account for uncertainty in noisy estimates of landscape variables (Dudaniec et al. 2016). In their comparison of microsatellite genetic data sets with maps of current density derived using circuit theory, Marrotte et al. (2017) found that current density was not usually a good predictor of gene flow for 4 terrestrial mammal species in Ontario, especially where habitat amount was high or pinch points were observed. Overall, these and numerous other efforts to extend circuit theory underscore its foundational and future importance to landscape genetics.

Identifying and Conserving Pathways and Corridors for Animal Movement

Circuit theory was quickly taken up and applied by conservation scientists and ecologists not only to predict population-level patterns of gene flow, but also to understand how landscape features influence individual movement paths and thus conservation and restoration of habitat corridors and targeted studies of movement (Dickson et al. 2013). The breadth of applications, along with comparative method studies, has increased understanding of the strengths of circuit theory in conservation and highlights its complementarity with other methods for predicting movement, including least-cost paths (e.g., Howey 2011; Mateo-Sanchez et al. 2015; Marrotte & Bowman 2017). Circuit theory is particularly appropriate when the assumption of moving individuals having limited knowledge of the surrounding landscape is met (McClure et al. 2016; Keeley et al. 2017; Maiorano et al. 2017).

Circuit theory's basis in random-walk theory results in an implicit assumption that individuals moving across a landscape have no knowledge of relative resistance beyond their immediate surroundings, making it particularly appropriate for modeling natal dispersal paths (McRae et al. 2008). Applications to predicting dispersal corridors for large, wide-ranging carnivores have been common (e.g., Proctor et al. 2015; Ahmadi et al. 2017; Gantchoff & Belant 2017; McClure et al. 2017), but circuit theory has also been used to model amphibian dispersal via surface water networks of Australia (Bishop-Taylor et al. 2015), dispersal paths of subterranean beetles via substratum karst systems (Rizzo et al. 2017), marine shrimp larvae dispersal via ocean currents (Dambach et al. 2016), dispersal of early human populations in Africa and the Caucasus (Tassi et al. 2015; Tarkhnishvili et al. 2016), and even pathways of early explorers (e.g., Hernando de Soto's route through the Appalachian Mountains in 1540 [Thayn et al. 2016]). Advantages of circuit theory may be less pronounced when applied to the movements of individuals through known

landscapes. For example, circuit theory and least-cost path models perform comparably in predicting seasonal ungulate migration routes (Poor et al. 2012; McClure et al. 2016). Still, circuit theory is suitable for characterizing relative frequency of routine movements along multiple potential paths through urban and other fragmented landscapes (e.g., Braaker et al. 2014; Rödder et al. 2016; Grafius et al. 2017).

Given its utility for predicting high-use animal movement routes, researchers have applied circuit theory to evaluate alternatives for establishment of protected areas to enhance connectivity among populations (e.g., pumas [*Puma concolor*] in the Atlantic Forest of southeast Brazil [Castilho et al. 2015], forest understory birds in Costa Rica [Fagan et al. 2016], and giant pandas [*Ailuropoda melanoleuca*] in China's Qinling Mountains [Wang et al. 2014]). Circuit theory models have also been used to identify corridors between occupied and unoccupied habitat areas to promote recolonization of a species' historic range, or to identify areas suitable for habitat restoration (e.g., Jarchow et al. 2016; Ziólkowska et al. 2016; Gantchoff & Belant 2017). Similarly, other applications have identified potential pathways for spread of invasive species, diseases, and pathogens (details given in Supporting Information).

Conservation scientists often wish to protect corridors that promote movement of more than 1 species and have used circuit theory to assess the functionality and efficiency of potential multispecies corridors (e.g., Koen et al. 2014; Bleyhl et al. 2017; Lechner et al. 2017). Several studies (e.g., Epps et al. 2011; Breckheimer et al. 2014) show that corridors designed for wide-ranging umbrella species enhance connectivity for less vagile organisms with similar habitat requirements, and Brodie et al. (2015) found that multispecies corridors tailored to ecologically similar species (e.g., carnivores and herbivores) can be highly effective for all species. Dilkina et al. (2017) explored the cost-effectiveness of grizzly bear (*Ursus arctos*) and wolverine corridors by optimizing corridor selection under a constrained budget. Even greater generality can result from species-agnostic approaches to estimating ecological flows that base landscape resistance on the degree to which habitats are unaltered or otherwise modified by humans (e.g., Bennie et al. 2014; Dickson et al. 2017).

Anthropogenic Barriers to Connectivity

Circuit theory has been used to determine how humans impact movement corridors and where mitigating these impacts might be most crucial to maintaining or restoring connectivity. Understanding the effects of linear infrastructure such as transportation corridors and other barriers (e.g., international boundary structures and fence lines) on connectivity and gene flow was a primary impetus for McRae's interest in the theory and development

of Circuitscape (McRae 2006). Examples include work by Litvaitis et al. (2015) that explores the potential effects of roads on the movement of wide-ranging carnivores in New Hampshire and work by Naidoo et al. (2018) examining barrier effects on movement corridors for African elephants (*Loxodonta africana*). Guidance for direct application of these approaches with transportation agencies has been provided by Beier et al. (2011), and initial explorations are underway that explicitly incorporate volume of traffic on highways into estimates of landscape permeability (e.g., Theobald et al. 2012). Yet, work integrating connectivity across transportation infrastructure, particularly within the context of regional transportation planning, remains understudied (e.g., Mateo-Sanchez et al. 2014), and this gap is especially important given the ubiquity of transportation and its strong population and genetic effects on various animals globally (Trombulak & Frissell 2000). Beyond the impacts of transportation corridors, circuit-theory applications have addressed a wide range of anthropogenic impacts on connectivity, including urbanization, agriculture, and energy infrastructure (Supporting Information).

More recent studies have assessed the vulnerability of populations to climate change due to fragmentation that could potentially impede adaptive shifts in distributions (e.g., Leonard et al. 2017a). A number of studies used Circuitscape to explicitly plan for climate-driven movements. For example, Lawler et al. (2013) used species distribution models to map the routes that organisms might follow to track shifting climates, and Littlefield et al. (2017) mapped connections between climatic conditions today and where those conditions will be in the future (i.e., climate analogs). These and other studies have used Circuitscape to model climate, sea-level rise, range shifts, and projections of climate-driven landscape change to determine or anticipate the impact of climate change on species and their movements.

Nontraditional and Emergent Applications of Circuit Theory

Fire Spread

Circuit theory has provided an intuitive analogue to the process of wildfire movement (i.e., spread) across heterogeneous landscapes. The approach accommodates important stochastic properties of wildfire by modeling probabilistic spread between adjacent neighbors in a landscape network (Gray & Dickson 2015). Circuit theory also accommodates the critical role of spatial context in estimating fire likelihood because areas on the landscape can burn far away from an ignition source. In this case, circuit conductance (the inverse of resistance) is a surrogate for the ease of fire spread across the landscape. Fuels, topography, and other biophysical variables that influence the spread of fire may be flexibly integrated into a conductance surface in a circuit-theoretic model (Gray

& Dickson 2015, 2016). Resulting metrics (e.g., current density and centrality) and maps of potential fire connectivity can be used to target areas on the landscape where fuel breaks could most effectively hinder fire movement through wildlife habitat (Welch et al. 2015) and disrupt the invasive grass-fire cycle (Gray & Dickson 2016). In addition, wall-to-wall estimates of fire connectivity can be useful to identify areas of highest fire likelihood across a landscape and, consequently, the natural and human infrastructure at greatest relative risk from wildfire (Gray & Dickson 2015).

Water Flow

The electronic circuit analogy has been used in a variety of subdisciplines within the field of hydrology. As early as 1962, electronic circuit models were seen as an innovative approach to analyzing groundwater flows (Robinove 1962). In these early studies, physical circuit models, often involving the careful placement and soldering of thousands of resistors for each individual run, were constructed in the laboratory to simulate the groundwater system (Miley & Kuelske 1990). With increased computer processing power, this approach was supplanted by more contemporary node-based numerical models that are in wide use today (Fetter 2001). The use of such models has significantly advanced scientists' understanding of flow connectivity within aquifers as well as between ground and surface waters (Singh 2014). Application of resistance-based groundwater models has provided insights into questions that are highly relevant to the field of conservation science, including understanding water budgets in the midst of rapid human development (Tillman et al. 2016), the effects of flow management (Shafroth et al. 2010), groundwater pumping (Falke et al. 2011) on dryland stream habitats and riparian ecosystems, and the impacts of climate change on stream summer base flows (Huntington & Niswonger 2012).

Ecosystem Services

In the context of ecosystem services, circuit theory has been used to examine the landscape genetic structure and movements of pollinators, especially bees, in response to habitat and land-use changes (e.g., Goulson et al. 2011; Lander et al. 2013; Lozier et al. 2013; Jaffe et al. 2016a, 2016b). In southeastern Australia, Luck et al. (2014) used Circuitscape to investigate the potential movements of Regent Parrots (*Polytelis anthoepus*) through almond orchards, which may benefit from parrots foraging on nuts remaining after harvest, reducing the need for manual or mechanical removal. Koh et al. (2013) used circuit theory to estimate the potential flow of agricultural insect predators across habitat networks in the U.S. Midwest. They quantified the pest-control benefit

of grassland restoration and native prairie remnants and concluded that the flow of multiple predators on soybean aphids (*Aphis glycines*) was improved by the presence of adjacent, native "conservation plantings" that maximize such biocontrol services.

Impacts of Circuit Theory and Future Opportunities

Circuit theory's widespread application across multiple disciplines (beyond genetics and wildlife ecology) is a testament to its power and flexibility as a tool for exploring movement and flow across a range of scales and settings. For example, novel applications of the theory to understanding the spread of fire, water, diseases, and invasive species, as well as the future impacts of climate change on natural and human systems, are transforming the way scientists, planners, managers, and decision makers think about or incorporate connectivity processes into their work. From these diverse applications, we anticipate that new areas of inquiry and tools will emerge that can also benefit the field of conservation.

We see a variety of opportunities for circuit theory's continued development and use in conservation. First, a new wave of applications is emerging from advances in how we conceptualize connectivity, such as by recognizing that a range of habitat conditions can serve as a source for individuals (and genes) moving between populations. "Omnidirectional" or "wall-to-wall" approaches (e.g., Walpole et al. 2012; Koen et al. 2014; Pelletier et al. 2014; Anderson et al. 2016; McRae et al. 2016; Supporting Information) avoid the need to arbitrarily define and delineate discrete areas to connect (e.g., habitat cores or patches), revealing important areas for connectivity over continuous landscape gradients. Because circuit theory extends easily to nontraditional landscapes, efforts to quantify connectivity in other dynamic systems, such as seascapes, riverscapes, and belowground environments (e.g., caves or karst), are expanding. Circuit theory can also be used to identify key places for mitigating or restoring connectivity (e.g., McRae et al. 2012; Torrubia et al. 2014) in areas where new investments in transportation infrastructure might prioritize crossing structures for wildlife. Second, tighter coupling between near real-time data on landscape dynamics (e.g., derived using remotely sensed images within Google's Earth Engine environment) and estimates of landscape resistance and current flow, as well as increasingly available information (e.g., Global Positioning System or other telemetry data) specific to the movement behaviors or seasonal life-history traits of a target organism, will greatly improve insights into or tests of potential connectivity. Third, we expect that outputs from Circuitscape will be used more frequently as hypotheses to strategically inform the design and monitoring of habitat-use studies and to strengthen statistical inferences drawn from field data.

Although circuit theory provides a robust and intuitive framework for analyses of gene flow, animal movement, and corridor use, IBR may not perform as well as some other frameworks (e.g., isolation by distance) in less fragmented landscapes (Ruiz-Gonzalez et al. 2015) or when connectivity is being assessed for migration pathways as opposed to dispersal pathways (e.g., Poor et al. 2012; McClure et al. 2016). As with any modeling framework, the assumptions and utility of a circuit-theoretic approach should always be assessed on a project-by-project basis. Several assumptions and caveats still need to be addressed, such as modeling long-distance dispersal events (McRae 2006) and asymmetric migration (McRae et al. 2008; but see Hanks 2017). Future applications of circuit theory could account for temporal variation in dispersal rates (Anderson et al. 2010; Cushman & Lewis 2010) and predicting patterns of variation at adaptive loci (e.g., Creech et al. 2017).

Since the initial applications of circuit theory in conservation, Circuitscape and other related applications have undergone rapid and near constant refinement and improvement. Increasingly, circuit theory-based analyses are being conducted on larger and more complex data sets through recent advances in open-source software (e.g., gflow [Leonard et al. 2017b]), programming (e.g., the Julia numerical computing language [Bezanson et al. 2017]), and cluster- or cloud-based computing resources. The Julia implementation of Circuitscape (version 5.0) has greatly improved performance and scalability. Users are now able to solve for landscape grids that are larger or derived at finer resolutions than those used in earlier versions, as well as pairwise resistance calculations between a higher number of focal points (see also, Supporting Information).

Similarly, advances in data visualization tools have assisted the communication of circuit theory results to a broader set of conservation practitioners, stakeholders, and planning efforts. A leading example is Migrations in Motion (<http://maps.tnc.org/migrations-in-motion>), which uses a dynamic illustration of projected species migrations under climate change (Lawler et al. 2013) and has been a powerful and accessible way for The Nature Conservancy (TNC) to communicate the potential risks of climate change to a variety of audiences, including the general public. These advances are often occurring as scientists around the world apply circuit theory to inform applications and decision makers. In his work at TNC, McRae played a major role in the development of generalized connectivity maps produced with wall-to-wall (Anderson et al. 2016) and Omniscape (McRae et al. 2016; Supporting Information) versions of Circuitscape models. These regional-scale flow maps remain a key component in TNC's Conserving Nature's Stage approach for identifying land protection priorities, which to date has helped guide decisions on US\$38 million in land protection funding. In India, national policy associated with

the Wildlife Protection Act, which delineates key habitat areas as tiger reserves, has been informed by Circuitscape-derived models and maps (Qureshi et al. 2014; Dutta et al. 2016).

We believe the impact of circuit theory and Circuitscape on conservation has come from not only the theoretical basis and elegance of the approach, but also from the powerful collaborations and active user community that have emerged. Because circuit theory took root so quickly and broadly, it can be expected to continue to provide a springboard for ecological understanding and remain an important tool for future researchers and conservation practitioners around the globe.

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Supporting Information

Additional topic areas and examples of the use of circuit theory or Circuitscape software and numerical computing methods (Appendix S1) and a sample gallery of map-based outputs (Appendices S2 and S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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