Three steps to strengthen confidence in connectivity models

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January 20, 2023

Abstract

Maintaining and restoring ecological connectivity is considered a global imperative to help reverse the decline of biodiversity. To be successful, practitioners need to be guided by connectivity modeling research that is rigorous and reliable for the task at hand. However, the methods and workflows within this rapidly growing field are diverse and few have been rigorously scrutinized. We propose three procedural steps that should be consistently undertaken and reported on in connectivity modeling studies in order to improve rigour and utility: (1) describe the type of connectivity being modeled, (2) assess the uncertainty and sensitivity of model parameters, and (3) validate the model outputs, ideally with independent data. We reviewed the literature to determine the extent to which studies included these three steps. We focused on studies that generated novel landscape connectivity outputs using circuit theory. Among 181 studies meeting our search criteria, 39% communicated the type of connectivity being modeled and 18% conducted some form of sensitivity or uncertainty analysis (or both). Only 19% of studies attempted to validate their connectivity model outputs and only 7% used fully independent data. Our findings highlight a clear need and opportunity to improve the rigour, reliability, and utility of connectivity modeling research. At a minimum, researchers should be transparent about which, if any, of these three steps were undertaken. This will help practitioners make more informed decisions and ensure limited resources for connectivity conservation and restoration are allocated appropriately.

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ABSTRACT

Maintaining and restoring ecological connectivity is considered a global imperative to help reverse the decline of biodiversity. To be successful, practitioners need to be guided by connectivity modeling research that is rigorous and reliable for the task at hand. However, the methods and workflows within this rapidly growing field are diverse and few have been rigorously scrutinized. We propose three procedural steps that should be consistently undertaken and reported on in connectivity modeling studies in order to improve rigour and utility: (1) describe the type of connectivity being modeled, (2) assess the uncertainty and sensitivity of model parameters, and (3) validate the model outputs, ideally with independent data. We reviewed the literature to determine the extent to which studies included these three steps. We focused on studies that generated novel landscape connectivity outputs using circuit theory. Among 181 studies meeting our search criteria, 39% communicated the type of connectivity being modeled and 18% conducted some form of sensitivity or uncertainty analysis (or both). Only 19% of studies attempted to validate their connectivity model outputs and only 7% used fully independent data. Our findings highlight a clear need and opportunity to improve the rigour, reliability, and utility of connectivity modeling research. At a minimum, researchers should be transparent about which, if any, of these three steps were undertaken. This will help practitioners make more informed decisions and ensure limited resources for connectivity conservation and restoration are allocated appropriately.

Keywords: biodiversity, circuit theory, Circuitscape, connectivity, conservation, sensitivity analysis, uncertainty, validation

INTRODUCTION

A 2019 global assessment by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services estimated that up to one million species around the globe are at risk of extinction (Brondizio et al. 2019). Preventing this large-scale biodiversity decline will require action to reduce the intensity of its underlying drivers: habitat loss, degradation, and fragmentation (Newbold et al. 2015). These drivers collectively exacerbate the problem by impeding species movement, or ecological connectivity, which is necessary to allow individuals to access food and water, establish new territories, supplement existing populations, avoid predators, and to find breeding partners (Hilty et al. 2020). In addition, reduced connectivity will inhibit species' ability to shift ranges and adapt to climate change effects (Thomas et al. 2004; Heller & Zavaleta 2009; Hannah 2011). Consequently, Parties to the Convention on the Conservation of Migratory Species of Wild Animals (CMS; 2020), a multilateral environment agreement under the United Nations, reaffirmed that maintaining and restoring ecological connectivity is one of their top priorities.

The need to identify areas important for connectivity spurred a proliferation of connectivity modeling studies (Correa Ayram et al. 2016), while the introduction of free and user-friendly tools such as Condatis (Wallis & Hodgson 2015), Linkage Mapper (Gallo & Greene 2018), Unicor (Landguth et al. 2012), and Circuitscape (McRae et al. 2008) made modeling connectivity more broadly accessible. Although the wide interest in, and application of, connectivity modeling is generally a positive development, it has fostered an abundance of literature that includes an overwhelming array of modeling methods and workflows (Zeller et al. 2012), few of which have been rigorously scrutinized (Wade et al. 2015; Zeller et al. 2018).

Given the limited resources available for implementing connectivity conservation actions, it is crucial that sound and transparent evidence underpin conservation prioritizations and actions (Elliot et al. 2014; McClure et al. 2016; Carroll et al. 2020). Furthermore, evaluating and weighing the evidence would be far easier if studies implement steps that are considered to be crucial for maximizing model reliability (Spear et al. 2010; Sawyer et al. 2011; Zeller et al. 2012; Wade et al. 2015; Abrahms et al. 2017; Laliberté & St-Laurent 2020). These steps include: (1) articulating the type of connectivity being modeled, (2) evaluating how much model output changes in response to uncertainty in the input parameters, and (3) validating the resistance surface and especially the connectivity model outputs. Here we report the results of a literature review focused specifically on if and how studies implemented any of these three steps.

Articulating the type of connectivity being modeled

Study goals should dictate, and clearly articulate, the type of connectivity that needs to be modeled at the outset (Allen & Singh 2016; Diniz et al. 2020). There are several types of connectivity, including daily foraging, seasonal migrations, dispersal/genetic, or range shifts, each of which correspond to a type of movement that operates at different spatial and/or temporal scales (Wade et al. 2015). For example, daily habitat connectivity pertains to movements by individuals to meet daily food, water, and shelter needs, whereas range shift connectivity focuses on movements that enable species to track habitat that is shifting due to climate change. The relevant spatial and temporal grains and extents clearly differ between those two types of connectivity; hence the need to clearly define what type of connectivity is being modeled and to select model inputs accordingly (Laita et al. 2011; Elliot et al. 2014).

Sensitivity and uncertainty analysis

Evaluating how much model output changes due to uncertainty among input parameters constitutes "uncertainty analysis" (Beier et al. 2009). This is technically different from sensitivity analysis, which evaluates which input parameters have the greatest influence on model output (Beier et al. 2009). Although the specific goals of uncertainty analysis and sensitivity analysis differ, in practice they are often implemented simultaneously. For example, the process of systematically varying the values of input parameters and quantifying how it affects variation in outputs can simultaneously serve as both uncertainty and sensitivity analysis (e.g., Marrec et al. 2020). The key is to articulate how the parameters in question relate to uncertainty or knowledge gaps. For simplicity, we will henceforth refer to these analyses collectively as sensitivity and uncertainty analysis (SUA).

Many authors have highlighted the importance of SUA, in part because there are many sources of uncertainty to consider in connectivity modeling, and because of the many decisions and assumptions in the analysis process (Wade et al. 2015). For example, using cougar GPS telemetry data, Zeller et al. (2017) showed that connectivity model outputs, including predicted locations for road crossings, were sensitive to the number of geospatial layers, the number of classes in categorical geospatial data (thematic resolution) and the spatial resolution of the geospatial data used when constructing the resistance surface. Using circuit theory based approaches to connectivity modeling, Bowman et al. (2020) showed that the range of cost weights within cost surface maps influenced the spatial distribution of current density. This narrowed the range of input cost weights and tended to spread current across the landscape, whereas current tended to be more concentrated when a broader range of cost weights were used.

Model validation

Given the many assumptions and sources of uncertainty inherent to connectivity models, perhaps the most important step in the analysis process involves validation of inputs (e.g., resistance surface) or more importantly, outputs (e.g., current density map, potential corridors) (Zeller et al. 2018; Carroll et al. 2020; Laliberté & St-Laurent 2020). For example, a study with an objective to help identify specific linkages for protection or locations along roads for overpasses or fencing generates an obvious need to validate model predictions with real-world movement or even presence/absence data (Xu et al. 2019; Cerqueira et al. 2021). However, if the study's aim is to assess the overall degree of connectivity of a landscape, then model predictions could be validated with inferential data such as genetics and biogeochemical markers (Wade et al. 2015). In either case, truly independent data would ideally be used; in practice these data are costly and time consuming to obtain. As a result, data used for validation vary in type and degree of independence, with implications for the reliability of model predictions (Spear et al. 2010; McClure et al. 2016). In the case of telemetry-based connectivity models, a portion of individuals, or relocations, could be withheld from the modeling procedure and used to validate results (but see Roberts et al. 2016).

Methodological shortfalls in the connectivity modeling literature have been reported for about a decade (Zeller et al. 2012; Wade et al. 2015; Laliberté & St-Laurent 2020), so we were hoping to see evidence of these shortfalls being addressed in more recent studies. Thus, in addition to evaluating if and how studies addressed the preceding procedural steps, we assessed whether the frequency of studies attending to these steps has changed over time. We focused our review on studies of terrestrial mammals (including bats) that used circuit theory in the time since it was first popularized as an approach to assess connectivity with the introduction of Circuitscape (McRae et al. 2008). Circuitscape is one of the most widely used connectivity modeling tools in recent years, appearing in 80 publications in 2017 alone (Dickson et al. 2019). We assume that the practices used in this subset of studies are representative of connectivity modeling studies in general.

METHODS

Literature Search

We used the Web of Science® database (WoS) to find publications that used circuit theory for landscape connectivity modeling. We accessed WoS on March 1st, 2022, and found all publications that had cited McRae et al.'s *Using Circuit Theory to Model Connectivity in Ecology, Evolution, and Conservation*(2008) up until Dec 31st, 2021. We refined the resulting list to only include studies that generated novel landscape connectivity outputs using circuit theory and that focused on one or more species of terrestrial mammal, including bats. Studies that modeled multispecies connectivity for a suite of taxa, mammalian or otherwise, were accepted so long as at least one terrestrial mammal was included.

Literature Assessment

For each study we recorded whether the researchers stated what type of connectivity was being modeled, and for those that did, we categorized the studies according to the following types: foraging, seasonal migrations, dispersal/genetic, or range shifts. If the type was not stated, it was recorded as non-specific.

We determined whether some form of SUA was conducted, and if so, we recorded the sources of uncertainty that were evaluated (e.g., resistance values, grid resolution). We also noted whether a factorial design was used in the SUA. A factorial design enables the simultaneous assessment of the influence of multiple factors within the SUA, including any interactions.

We then determined whether model validation was conducted, and if so, we noted (i) whether validation was conducted on the layers used to derive connectivity models (henceforth "input layers,", e.g., habitat layers or resistance surfaces) and / or on the "output layers" from the connectivity model itself (i.e., the current density map produced using circuit theory) (ii) the type of data that were used for validation (tracking, genetic, camera trap, point occurrence, or expert opinion) (Table 1). If a study used more than one type of data for validation, we recorded the type that is deemed to be associated with least uncertainty according to the hierarchy presented by Wade et al. (2015) (iii) the degree of independence of the data used for validation (categories: not independent, partially independent, fully independent), and (iv) the degree of agreement between model predictions and validation data. The latter results were taken at face value from authors' written interpretation of their validation analysis and generalized as either "positive" or "negative." If authors found their models had mixed ability to predict validation data, or if the results of the validation were not clearly presented, they were categorized as either "mixed" or "inconclusive," respectively. For our purposes, "mixed" included multispecies studies that found success in modeling movement of one studied species, but not all.

We cross-tabulated studies according to the type of data used for validation and the degree of independence of the data used for validation.

Temporal trends in modeling practices

We first tallied the number of studies that met our criteria in each publication year. We then qualitatively evaluated whether practices have changed in time by plotting line graphs of the proportion of studies in each year that fell into each of the assessment categories. For instance, we calculated the proportion of studies in each year that conducted some form of SUA and noted any obvious trend.

RESULTS

Literature search

We found 884 studies that cited McRae et al. (2008) in our literature search. Of those, 181 met our criteria of having novel landscape connectivity outputs generated using circuit theory (Figure 1) and that focused on one or more species of terrestrial mammal. The Supporting information provides details for each study.

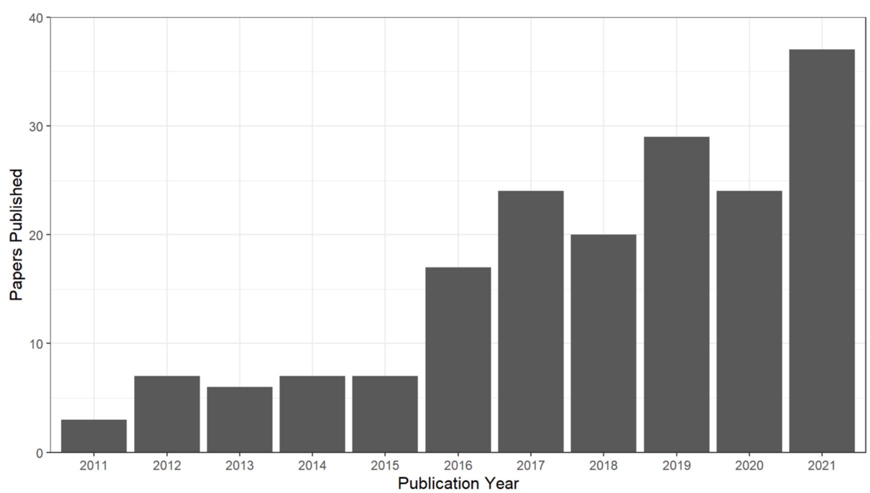

Figure 1. The number of studies published each year that used circuit theory to model connectivity for at

least one terrestrial mammal.

Articulating the type of connectivity being modeled

One-hundred and ten of the 181 studies (60%) were non-specific regarding the type of connectivity they intended to model. Of the seventy-one studies that did communicate a type of connectivity, 54 (76%) indicated they were modeling genetic connectivity / dispersal facilitation, 10 (14%) specified seasonal migration, 3 (4%) specified within-home range movements, and 4 (6%) specified range shifts.

Sensitivity and uncertainty analysis

Thirty-three (18%) of the 181 studies conducted some form of SUA. Of those that conducted a form of SUA, most evaluated the sensitivity of model output to: (i) variation in resistance values used in the resistance surface layer (ii) the number of connectivity focal nodes ("points or regions between which connectivity is to be modeled") (McRae et al. 2013), or (iii) inclusion of particular landscape variables (e.g., slope, canopy cover, distance to disturbance).

Model validation

Of the 181 studies reviewed, 80 (44%) included no validation step at all; i.e., they validated neither their input (habitat or resistance) layers nor their connectivity output (current density) layers. Fifty-five of the 181 studies (30%) validated their habitat layers that were used to generate the resistance surface layers used in the connectivity analyses. Twelve studies (7%) validated their resistance surface layers that are input into Circuitscape, and only 34 (19%) validated the results of their connectivity model (the current density output layer).

The most common type of data used in the validation step was point occurrence (60 studies; Table 1), followed by tracking (25), genetic (10), camera trap (4), and expert opinion (2). Of the 101 studies that performed some form of validation, only twenty used fully independent data, including expert opinion. Twenty-seven studies used partially independent data and the remaining 54 used non-independent data, most commonly withholding a subset of locations or paths for cross-validation. Fully independent data were used in five studies to validate their habitat layers and in three studies to validate their resistance/permeability layers. Only twelve studies out of the 181 (7%) included in this assessment used fully independent data to validate the results of their connectivity analysis, the current density output.

Table 1 . Cross-tabulation of studies according to the type of data used for validation and the degree of independence of validation data. Numbers in parentheses are for studies that validated the model output (current density layer), and remaining numbers represent studies that validated a model input (habitat or resistance layer).

Degree of data independence	Tracking Data	Point Occurrence	Genetic	Camera Trap	Expert Opinion	Total
Non	6(11)	32(2)	3			41(13)
Partially	1(4)	14(2)	2	1(3)		18(9)
Fully	(3)	4(6)	2(3)		2[a]	8(12)
Total	7(18)	50(10)	7(3)	1(3)	2	67(34)

[a] Although we categorized Expert Opinion as a fully independent data source, it differs from other categories because it is not empirical (Zeller et al. 2012).

Twenty-two of the 34 studies that validated their current density (output) models (~65%) reported agreement between model predictions and validation data, while four (12%) found poor agreement between model results and validation data. The remaining eight (~24%) either reported mixed results or were inconclusive.

After an initial and substantial increase, the proportion of studies that specified the type of connectivity being modeled leveled off or even declined in recent years (Figure 2). Studies that implemented some form of SUA seem to have been slowly increasing, and there has been no clear trend through time in the proportion of studies validating connectivity models (Figure 2).

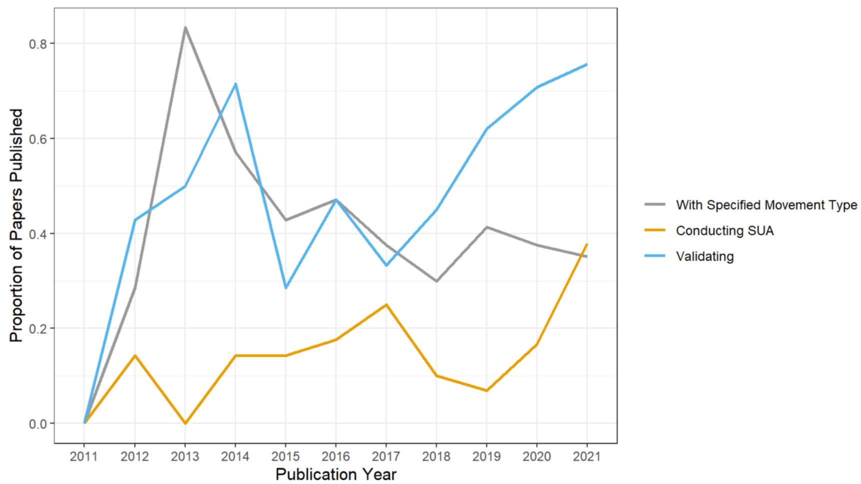

Figure 2. Proportion of publications within each year that conducted any of the three main methodological steps: (1) specifying the type of movement / connectivity being modelled, (2) conducting some form of sensitivity and / or uncertainty analysis, or (3) conducting some form of validation.

DISCUSSION

We reviewed 181 studies that generated novel landscape connectivity outputs using circuit theory and found that while such user-friendly programs are being widely used, researchers are typically not (i) clearly articulating the type of connectivity being modeled (ii) conducting some form of sensitivity or uncertainty analyses, and (iii) validating the connectivity model output.

Articulating the type of connectivity being modeled

Fewer than half of the studies we reviewed included a description of the type of connectivity being modeled. Examples of those that did include Xu et al. (2019) who clearly indicated that they were modeling connectivity for seasonal migrations of Tibetan antelope (*Pantholops hodgsonii*); Alexander et al. (2019) who stated they were interested in connectivity for dispersal and gene flow of giant kangaroo rats (*Dipodomys ingens*); and Di Febbraro et al. (2019) who predicted range shifts of alien squirrel species due to climate change and land use change.

Being clear about the type of connectivity is crucial because it determines the type of data that should be used to parameterize and validate the model, as well as the resulting conservation implications. Indeed, different types of data would be required to predict connectivity for within-home range movement *versus* range shifts, migrations, or dispersal (Wade et al. 2015; Aylward et al. 2020). For example, Keeley et al. (2017) found that connectivity models based on home-range habitat-use data were ineffective at predicting connectivity for dispersal and mating movements. Several studies, however, were careful to use location data from outside of home ranges (e.g., Merrick and Koprowski 2017; Popescu et al. 2021) or data only from dispersing individuals (Carroll et al. 2020).

Sensitivity and uncertainty analyses

Connectivity analysis workflows are characterized by numerous analytical decisions (often arbitrary), myriad assumptions, and a variety of widely-recognized sources of uncertainty (Bowman et al. 2020). For these reasons there have been repeated calls to include SUAs in connectivity studies (Sawyer et al. 2011; Zeller et al. 2012, 2017; Wade et al. 2015). Nevertheless, we found that only 19% of the 181 studies we reviewed conducted some form of sensitivity or uncertainty analysis.

Among studies that have implemented SUA, researchers found that important and substantial sensitivities are commonplace. For example, Churko et al. (2020) found that the current maps generated for amphibian species in Switzerland were highly sensitive to the choice of transformation applied to the input resistance layers. Marrec et al. (2020) used a factorial design to explore interactions among uncertainty sources in their large-scale, species-agnostic analysis of landscape connectivity in Alberta. They found that whether water was included as a barrier had the single greatest effect on predictions, followed by the scaling function used for resistance values.

Of primary importance is assessing the degree to which predictions about landscape connectivity vary in response to variation in the input parameter values. In practice, and tailored by one's knowledge of the study system, the general approach is to: (i) identify the input parameters that most warrant scrutiny *via* SUA (e.g., the ranking of land cover types with respect to resistance) (ii) systematically vary parameter values (iii) use a factorial design to explore all unique parameter value (treatment) combinations (if more than one parameter is being examined) (iv) run the connectivity model using each unique parameter value combination, (v) quantify variation among the connectivity model outputs, and finally (vi) statistically analyze this variation in relation to the treatments. Exactly how variation among model outputs is quantified will depend on the goals of the study and will also govern the type of statistical method that is most suitable for the main SUA. For example, in their species-agnostic modeling of connectivity across Alberta, Canada, Marrec et al. (2020) used several complementary approaches, including one in which a correlation matrix was built using Pearson correlation coefficients from all pairwise comparisons of output layers from their factorial design. They then calculated a dissimilarity matrix from this correlation matrix, and used distance-based redundancy analysis (db-RDA) to evaluate the effects of their manipulated variables. One limitation was that they were unable to include interactions in their db-RDA due to overfitting concerns (Marrec et al. 2020).

Admittedly, computational demands may limit the number of parameters that can be explored within a fully factorial design. For instance, to have explored all possible landscape combinations for their study on the sensitivity of path selection function models and predicted road-crossing locations, Zeller et al. (2017) would have needed to create more than 5 million landscape definitions. Instead, the authors implemented a procedure that yielded 2500 combinations of inputs at random, and then used a multi-model inference and model averaging approach to infer the most important predictors of output variation (Zeller et al. 2017). This represents an effective alternative to fully factorial sensitivity analyses for which computational demands exceed capacity.

It is reasonable to ask whether SUAs are necessary if validation with independent data shows connectivity models to be suitably accurate. We believe that sensitivity analyses, in particular, could still be useful in this scenario because they can help identify which input variables have the greatest effect on the results, and should therefore be the focus of future research. For example, dispersal distances are fundamental to connectivity analyses (Liu et al. 2014) but are often estimated based on morphological traits (Tamme et al. 2014; Albert et al. 2017). Conversely, sensitivity analyses can also streamline analyses by identifying elements that can be simplified. For example, Bowman et al. (2020) found that current densities were generally insensitive to specific cost weights assigned to land cover categories so long as categories were ranked in the correct order.

Model validation

Although roughly half of the studies performed some form of validation, only 19% validated the output from the circuit analysis itself. Examples of studies that did conduct validation include Bond et al. (2017), who assessed the accuracy of the connectivity model output by determining whether the predicted wildebeest (*Connochaetes taurinus*) corridors contained more or fewer occurrence records than expected by chance. Similarly, Xu et al. (2019) compared Tibetan antelope migratory routes predicted by connectivity models to those actually used according to GPS collar data. Several studies used genetics as a form of inferential validation (cf., Wade et al. 2015), including a study by Epps et al. (2013), which found that connectivity estimates based on genetic data were consistent with connectivity estimates developed using occupancy / habitat use data for African elephants (*Loxodonta africana*). Carroll et al. (2020) used observations only from dispersing individuals and three different validation metrics to select the most accurate connectivity map from among six variations.

Other studies that included a validation step either validated the input habitat layer or the input resistance/permeability layer. Several used model selection/tuning tools (e.g., data resampling / cross validation, Akaike Information Criterion, etc.) to help assess or improve their habitat models (Pitman et al. 2017; Osipova et al. 2019; Zhang et al. 2019; Almasieh et al. 2019). While validating input layers adds a degree of rigor, it is not a substitute for post-modeling assessment of accuracy (Wade et al. 2015).

Only 20% of the studies that validated either their input or output layers did so using fully independent data (8 and 12 respectively). For example, Gantchoff et al. (2017) used an independent dataset of citizen-reported sightings of black bears (*Ursus americanus*) to validate the output from their connectivity model, while Koen et al. (2014) used independent empirical datasets of herptile road kill sites and fisher (*Martes pennanti*) telemetry to validate their current density map. Some studies split their data into training and validation datasets (McClure et al. 2016; Brennan et al. 2018). This approach is helpful for assessing model precision more so than accuracy (Warren et al. 2020), and in some instances could lead to model accuracy being overestimated when training and validation data are non-independent (Roberts et al. 2016).

A number of studies that either did not validate their model(s) or validated with non-independent data, cited a lack of independent data or the difficulty/cost associated with obtaining these data (e.g., Dutta et al. 2018). Advances in both genetic sampling and GPS tracking equipment are enabling the collection of more data at lower cost and the increasing availability of “open” movement data, such as those available in Movebank (Kranstauber et al. 2011; Wikelski et al. 2020), could provide a solution for some studies. Further, when input data are abundant, as is common with GPS telemetry, a portion of these data can be withheld to create pseudo-independent data for validation. However, the effectiveness of this approach hinges on the method by which these data are held back (random individual or random point), and accounting for inherent non-independence among data points that may bias validation results.

We acknowledge that there is no apparent consensus as to which is the ‘best’ method for validation (McClure et al. 2016; Zeller et al. 2018). As Goicolea et al, (2021) point out, it may be most prudent to use several methods to test different aspects of connectivity, as they did in their study on Iberian lynx.

Circuit-theory based models

While the purpose of this study was not to evaluate the accuracy of circuit theory models specifically, our assessment found that the output from those models were corroborated by validation in about 65% of the studies. However, that figure is not particularly reassuring considering (i) that only 19% of the studies attempted to validate their connectivity results, and (ii) the potential for bias against publishing studies with negative results (Fraser et al. 2018).

As Dickson et al. (2019) point out, current maps are an important component of The Nature Conservancy’s approach for identifying land protection priorities, which helped guide the use of $38 million (USD) of land protection funding. Nevertheless, without a well-designed validation procedure, there is clear potential for ineffective use of limited conservation resources and negative outcomes for the species of interest. LaPoint et al. (2013), for example, found that Circuitscape failed to predict movement corridors for fisher, which could have resulted in the wrong parcels of land being conserved. In an effort to identify potential wildlife crossing corridors and plan road mortality mitigation features for a road enlargement project, Laliberté et al. (2020) validated the results from both Circuitscape and LinkageMapper and found that Circuitscape predictions were less accurate for deer than for moose (*Alces alces*) corridors.

Trends over time

Although we did not perform any statistical analyses, we found no indication of any systematic improvement in communicating the type of connectivity being modeled, conducting SUAs, nor in validating model outputs. Indeed, based on our assessment of 181 studies, there has been little improvement since earlier, similar reviews. For example, Sawyer et al. (2011) found that only 9 of 24 studies using least-cost path analysis performed some form of model validation. In 2012, Zeller et al. (2012) reviewed 96 studies that estimated landscape resistance and found that most studies were not clearly describing or assessing the uncertainty associated with the input parameters nor with the output surfaces. A United States Department of Agriculture report published a few years later (Wade et al. 2015) concluded that "validation of connectivity maps is virtually non-existent" and as such, resulting connectivity maps should "be considered to be a largely untested hypothesis rather than a tested solution to a problem."

Potential issues with our assessments

We acknowledge several potential issues with our assessment. Firstly, we restricted our review to studies that used only circuit theory and as such our findings may not be representative of connectivity studies in general. However, user-friendly tools are also available for other approaches and we have no reason to believe that they would be applied in a systematically different way than for those that use circuit theory. Indeed, Sawyer et al. (2011) and Wade et al. (2015) found similar results for studies using least-cost paths.

Secondly, our classification scheme was devised to discretely categorize a wide variety of methods being used in connectivity modeling. Despite our attempt to ensure replicability of our review process, we acknowledge that our method relied on interpretation of (often brief) descriptions of validation procedure. We encourage researchers to make the details of their validation process unambiguous, as the nuances of these analyses may be important for ascertaining model reliability.

Finally, although there is an appreciable amount of model-based connectivity research on a diverse array of species (including insects, non-avian reptiles, birds, amphibians, plants, etc.), we chose to limit our scope to terrestrial mammals. We imposed this limitation so that our results would reflect studies that examined similar movement behavior (relative to aerial migration or seed dispersal, for example). For this reason, the proportions of validation data types and independence are not intended to reflect modeling efforts being done in non-mammalian ecology, although the importance of validation goes well beyond mammalian studies, as do the potential consequences of neglecting model validation.

Conclusion

Governments around the world agree that maintaining and restoring ecological connectivity is a key component of biodiversity conservation (e.g., Convention on Biological Diversity 2010; Convention on Migratory Species 2020). To target their conservation and restoration efforts appropriately, practitioners must be informed by rigorous and reliable connectivity modeling research. This requires, at a minimum, that researchers consistently articulate the type of connectivity being modeled, undertake sensitivity and uncertainty analyses, and validate the connectivity model outputs with independent data. We encourage connectivity modelers to be up-front and transparent about which, if any, of these steps have been completed, and reviewers of connectivity modeling manuscripts to request this information if it is lacking. These simple steps will enable consumers of the research, including practitioners, to more readily assess its reliability and utility. Without these measures, we risk mis-use of limited conservation resources and failing to meet key conservation targets.

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