Taking a moment to measure networks-an approach to species conservation

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Taking a moment to measure networks—an approach to species conservation

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Abstract

Context Network-theoretic tools contribute to understanding real-world system dynamics, such as species survival or spread. Network visualization helps illustrate structural heterogeneity, but details about heterogeneity are lost when summarizing networks with a single mean-style measure. Researchers have indicated that a system composed of multiple metrics may be a more useful determinant of structure, but a formal method for grouping metrics is still lacking.

Objectives Our objective is to present a tool that can account for multiple properties of network structure, which can be related to model outcomes.

Methods We develop an approach using the statistical concept of moments and systematically test the hypothesis that this system of metrics is sufficient to explain variation in processes that take place on networks, using an ecological system as an example.

Results Our results indicate that the moments approach outperforms single summary metrics by

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adjusted-R^2 and AIC model fit criteria, and accounts for a majority of the variation in process outcomes. *Conclusions* Our scheme is helpful for indicating when additional structural information is needed to describe system process outcomes such as survival or spread.

Introduction

Network theory is ubiquitous across the applied sciences (Boccaletti et al., 2006; Barthélemy, 2011; Blonder et al., 2012). Networks are appealing because they provide clear visualizations of inter-linked systems, and networks preserve heterogeneities and local information. The motivating hypothesis implicit in network analysis is that by understanding the underlying structure of linkages, researchers gain predictive power about processes taking place on networks, such as the dispersal and persistence of organisms (Urban et al., 2009), infectious disease dynamics (May, 2006), neuron communication (Laughlin and Sejnowski, 2003), and the diffusion of ideas (Watts, 2002).

Networks are often described using summary statistics such as mean degree, mean shortest path, and mean clustering coefficient (Albert and Barabasi, 2002; Newman, 2003; Estrada and Bodin, 2008). Summary statistics give an overview of the network linkages, but the relationship between summary statistics and processes is unclear *ex ante*. Furthermore, details about heterogeneities among networks vanish when summarizing networks with a single mean-style metric. An approach composed of multiple metrics could aid research in the analysis of network structures, but few studies group network metrics together in a formal way (Estrada and Bodin, 2008; Shanafelt et al., 2017). We address this gap in the literature by applying a set of network metrics (Shanafelt et al., 2017) to the problem of prairie dog conservation in North America. In doing so, we test the hypothesis that a set of simple metrics can sufficiently explain the variation in processes playing out on networks, better explaining model outcome than a single metric alone. The nested nature of our

approach is motivated by the statistical concept of moments, where a set of numerical features are systematically calculated and used to describe the structure of a distribution—or, in the case of a network, a set of connections among nodes—in increasingly cumulative detail.

Network science is awash with approaches for measuring the properties of networks (Albert and Barabasi, 2002; Newman, 2003; Rayfield et al., 2011). For example, Barrat et al. (2004) use the mean clustering coefficient, a measure of local cohesion defined by node degree and edge weights, to study the effects of topology and node interaction strength in a scientific collaboration network and the worldwide air-transportation network. Liu et al. (2013) use global efficiency, the inverse of the harmonic mean of the total number of pairwise shortest paths, to parse out the effects of Alzheimer's disease on human brain networks. Thompson et al. (2017) study the effects of node removal—either randomly or by shortest path criteria (betweenness centrality)—on the functioning and stability of ecological systems. Rayfield et al. (2011) highlight the popularity of summary indices in ecology, asserting that the number of publications using network theory to quantify habitat networks has grown tenfold over the past three decades. Many established metrics for measuring network connectivity are strongly correlated (Baggio et al., 2011), but less is known about how metrics complement each other to describe the complete structure of a network.

Specifically for landscape ecology, network theory has found a home with applications for habitat fragmentation, habitat management, and species conservation (among others). For example, Bunn et al. (2000) and Urban and Keitt (2001) build habitat graphs from spatial land cover data and develop a node removal algorithm to identify important nodes for network connectivity and species persistence. Pascual-Hortal and Saura (2006) test the effects of node removal on a suite of network properties. Mouquet et al. (2013) adopt the notion of node removal to develop the "keystone patch" concept. Urban and Keitt (2001), Minor et al. (2008), and Schick and Lindley (2007) combine network and metapopulation theory to model Mexican spotted owl, wood thrush, and Salmonid populations respectively. Friesen et al. (2019) use networks to inform marine protected area management in relation to regional hotspots; Phillips

et al. ([2008](#)) take a network approach to finding the optimal connectivity of a species habitat network, minimizing number of connections between habitat reserves while maximizing the area of connected habitat. For a general discussion of network theory in ecology and a brief overview of its many applications, we would direct the reader to Minor and Urban ([2008](#)), Urban et al. ([2009](#)), and Rayfield et al. ([2011](#)). For a more broad overview of network theory across the sciences, see Albert and Barabasi ([2002](#)) and Newman ([2003](#)). However, in landscape ecology, most studies reduce the network to a specific of specific summary metrics which, though they may capture general properties of landscape structure, lack a formal grouping.

We demonstrate our approach to measuring network structure using the statistical moments of "eigenvector centrality" (Borgatti, [2005](#); Shanafelt et al., [2017](#)). The spectral radius of a matrix is a fundamental measure in the analysis of social, biological, and infrastructure networks (van Mieghem, [2011](#)). Spectral radius faces the same limitations as any other single metric because it summarizes global network structure. However, derivation of the spectral radius also yields the eigenvector centrality, which normalizes the information on all the linkages in a network. Though it preserves a great deal of local information, a drawback of eigenvector centrality is that it does not provide a simple summary statistic. We jointly use spectral radius and eigenvector centrality, collectively known as eigenmetrics, to demonstrate our nested approach to measuring network structure. Specifically, we apply the concept of moments by treating the eigenvector centrality as a distribution of node connectivity scores. Different moments (e.g. mean, variance, skewness) of the resulting distribution highlight different topological properties of networks. The interplay among these network "moments" is useful for describing, and potentially predicting, processes occurring on networks.

In this paper, we present a general modelling approach to evaluate the impact of network structure on model outcomes such as spread or survival. First, we briefly outline the theoretical underpinnings of the approach. Then, we apply the framework to model prairie dog metapopulation dynamics. Prairie dog management is a vital component for the conservation of the black-footed ferret, a critically endangered species of the southwest United States (USFWS, [2013](#)).

Prairie dog metapopulations can be represented as a network of multiple habitats with distance as the dominating factor for successful dispersal (Roach et al., [2001](#)). Population growth is largely driven by variable, individual dispersal to spatially distinct prairie dog towns, so a simple mean field model may fail to capture important local information (Durrett and Levin, [1994](#)). We use an agent-based modeling approach to capture such dynamics over a network of prairie dog towns. Agent-based models (ABMs) are widely used in relevant studies on individual behavior, spatial population dynamics and conservation (Grimm and Railsback, [2005](#); West et al., [2011](#); Sibly et al., [2013](#); Schoon et al., [2014](#); Baggio et al., [2019](#)). Our results demonstrate the potential for the approach to be a standard method for grouping networks and parsing outcomes.

Materials and methods

In this section, we first present our approach for distinguishing network structure, which uses the concept of statistical moments to build a set of multiple, layered network metrics to define a clear picture of network structure. We hypothesize that our approach using multiple metrics will be able to better explain model outcome than an approach with a single metric alone. To test this hypothesis, we generate a large suite of network structures, and implement an agent-based model of a prairie dog metapopulation on these spatial networks. We analyze our results by comparing general trends in model outcomes between and across network metrics, and perform a series of regression models to investigate how different combinations of spectral radius and eigenvector centrality scores perform as predictors of prairie dog spread and survival. Finally, we test the robustness of our findings by conducting a sensitivity analysis of the parameters of the agent-based model.

Measuring a network using a nested moments approach

Consider a *weighted* network G with N nodes, where each pair of nodes is connected by an edge that represents the relative ease of movement or information spread through the network, with lower weights leading to less resistance on the network and easier

movement. The network G can be expressed as an $N \times N$ adjacency matrix, denoted A_G, where the edge weights between the N nodes of G make up the elements of A_G (Fig. 1a). A_G is always a zero-diagonal matrix, as information faces no resistance to stay at its current node. Edge direction can play a substantial role on network dynamics especially when dealing with issues of asymmetry (e.g., uphill and/or downhill transportation, (un)reciprocated contact, etc.). We develop our framework in the context of bidirectional networks, which are common in network science and landscape ecology (Urban and Keitt, 2001; Boit et al., 2012), but it can be generalized to directional networks by modeling inflows and outflows as separate edges.

The spectral radius, λ_G, is the dominant eigenvalue of A_G and measures the overall traversability across a network (Jacobi and Jonsson, 2011). In our context, where edge weight has a specific meaning (e.g., the distance that an individual of a species needs to go from node A to node B), a network with low spectral radius is less resistant and highly connected. An increase in the spectral radius indicates a decrease in connectivity. Spectral radius is a mean measure, so information—such as the distribution of poorly or highly connected nodes—is lost when it is used to summarize network characteristics. This may be acceptable for some analyses, but unacceptable for others. For a network with a given number of nodes and weighted edges, there is an infinite set of network configurations for any spectral radius, and these different configurations can lead to different outcomes (Fig. 1b). This problem is not unique to spectral radius. For example, many different disease outcomes are possible on networks with the same mean degree (May, 2006; Ames et al., 2011).

The adjacency matrix can also be used to calculate the eigenvector centrality scores (EC) of G, which describes the importance of an individual node within a network. The EC is the $N \times 1$ eigenvector ($\vec{v}_G$) associated with the spectral radius whose elements are rescaled such that the Euclidean norm of $\vec{v}_G$ is 1. The ith component of the EC ranks the importance of the ith node as donor and recipient of information within the network and describes its contribution to network connectivity (Borgatti, 2005; Urban et al., 2009). A node with a low EC score is highly connected relative to other nodes in the network. Note again that this interpretation is in the context of a network that

assesses the costs of movement and distance. It may not be the same for networks whose weight has a different meaning. Therefore, in our context, the EC provides a value for each node, but this does not help summarize the network. To summarize the EC, we treat the elements of an N-dimensional EC as N data points and use the statistical moments of the corresponding empirical distribution.

By building a network based on spectral radius as well as the statistical moments of the EC, we obtain a clearer picture of overall network structure. Indeed, this approach is similar to a taxonomic hierarchy, where as we move up the hierarchy from kingdom to phylum to class, all the way to species and subspecies, we refine the classification of an organism. Similarly, suppose that our view of the structure of the network is represented by a tree. If we start at the base (a mean measure of connectivity), then we have a limited view of the structure of the network. As we jointly add metrics, we move up the tree and obtain a more complete picture of the network, which we can relate to model outcome. While the concept is applicable to *all* network metrics, we specifically use the second and third moments of the eigenvector centrality scores. We discard the mean, the first moment, because there is a one-to-one relationship between EC mean and the second moment (Supplemental Material A). We build our picture of the network using two moments of the EC distribution, in addition to spectral radius as a base. In an *unweighted* network, one could do so from the mean, variance, and skewness of the degree distribution.

Variance (the second moment) measures the spread in a dataset. In a network context, EC variance ($\mathrm{var}(\vec{v}_G)$) measures the spread in node contribution across the network and provides a measure of heterogeneity among nodes. A zero EC variance implies that all nodes contribute equally to global connectivity (Fig. 1b). Networks with nonzero EC variance contain at least two nodes that contribute unequally (Fig. 1b).

Skewness, the third moment, indicates whether deviations from the mean of a dataset are systematically positive or negative and measures the level of asymmetry in data. In a network context, EC skewness ($\mathrm{skew}(\vec{v}_G)$) captures the net ratio of relatively strong to weak contributors. Networks with negative EC skewness possess a larger proportion of weak contributors (Fig. 1c), zero EC skewness, a
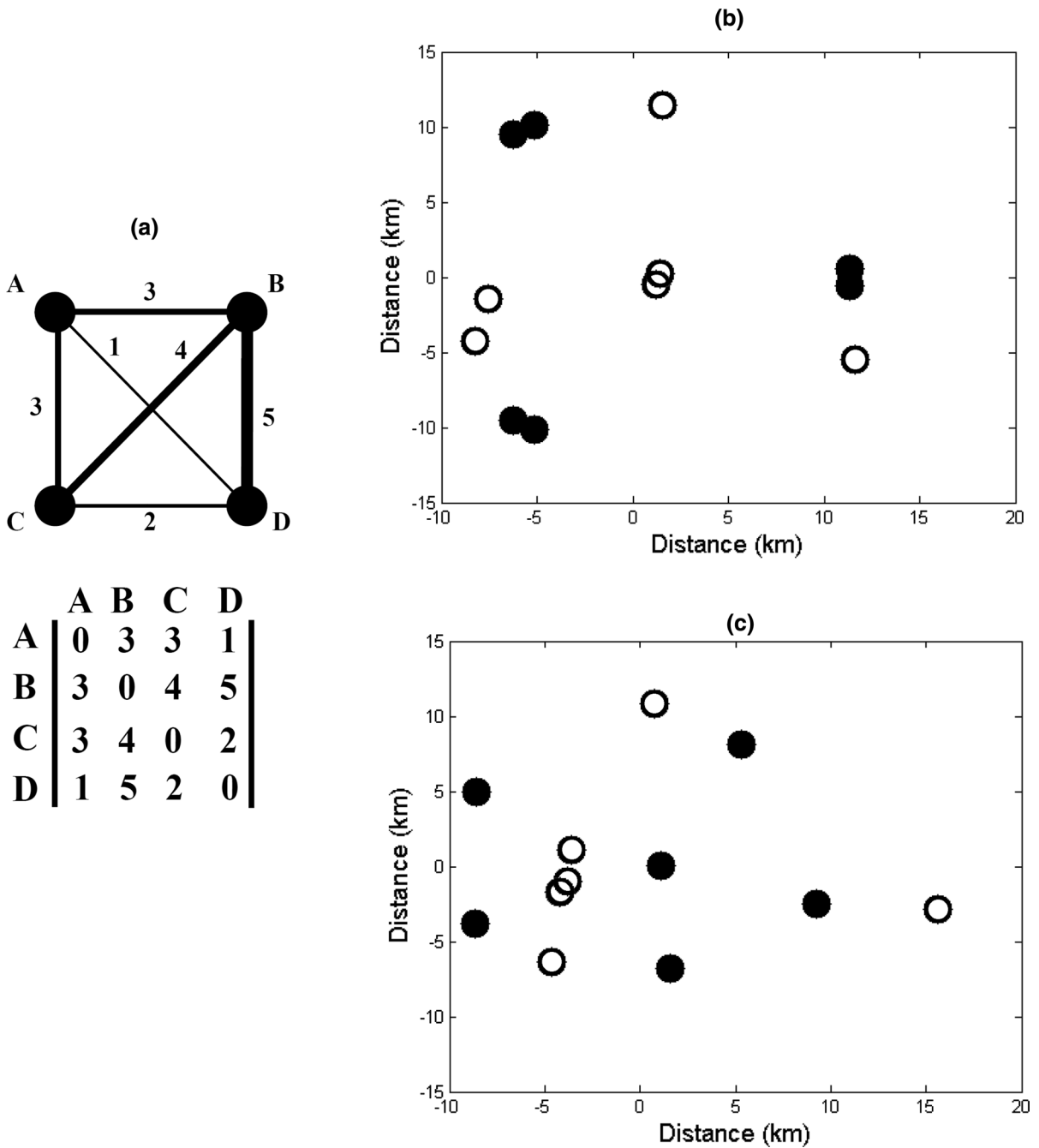
Fig. 1 Illustration of a different spatial networks. Panel **a** presents a weighted 4-node network denoted G and its corresponding adjacency matrix (A_G). The weights, denoted numerically and by edge width, act as facilitators/inhibitors of movement along some dispersal corridor between nodes. Panel **b** depicts two networks with equal spectral radius ($\lambda_G = 80$km), but different eigenvector centrality (EC) variance ($\text{var}(\vec{v}_G) = 0$); hollow nodes represent a network with a nonzero EC variance ($\text{var}(\vec{v}_G) = 0.026$). Panel **c** depicts two networks with equal spectral radius and EC variance ($\lambda_G = 65$km and $\text{var}(\vec{v}_G) = 0.0086$), but different EC skewness. Solid nodes indicate a network with a negative EC skewness ($\text{skew}(\vec{v}_G) = -1.79$); hollow nodes indicate a network with a positive EC skewness ($\text{skew}(\vec{v}_G) = 1.086$)

one-to-one ratio of weak to strong contributors, and network structures with positive EC skewness have a higher proportion of strong contributors (Fig. 1c). Our approach of using EC moments could be extended to higher order moments, but it is hard to produce clear interpretable meanings for statistical moments past the third (Casella and Berger, 2002).

While we focus on spectral radius and eigenvector centrality, our approach is by no means limited to them (Fig. 2, Table 1). One could build a system with more than three levels, or use a broad range of network metrics to capture specific, desirable aspects of a network's structure such as clustering or modularity

(Barrat et al., 2004; Newman, 2006). Many network metrics are correlated with each other (Estrada and Bodin, 2008; Rayfield et al., 2011). For example, spectral radius is positively correlated with the mean strength and the mean clustering coefficient of a network (Table 1; Supplemental Material B). By using a rescaling argument to derive the mathematical relationship between spectral radius and mean strength, one can relate mean strength to mean clustering coefficient by a constant factor. The latter implies a connection between spectral radius and mean clustering coefficient via transitivity. Additionally, EC variance is closely related to common metrics not
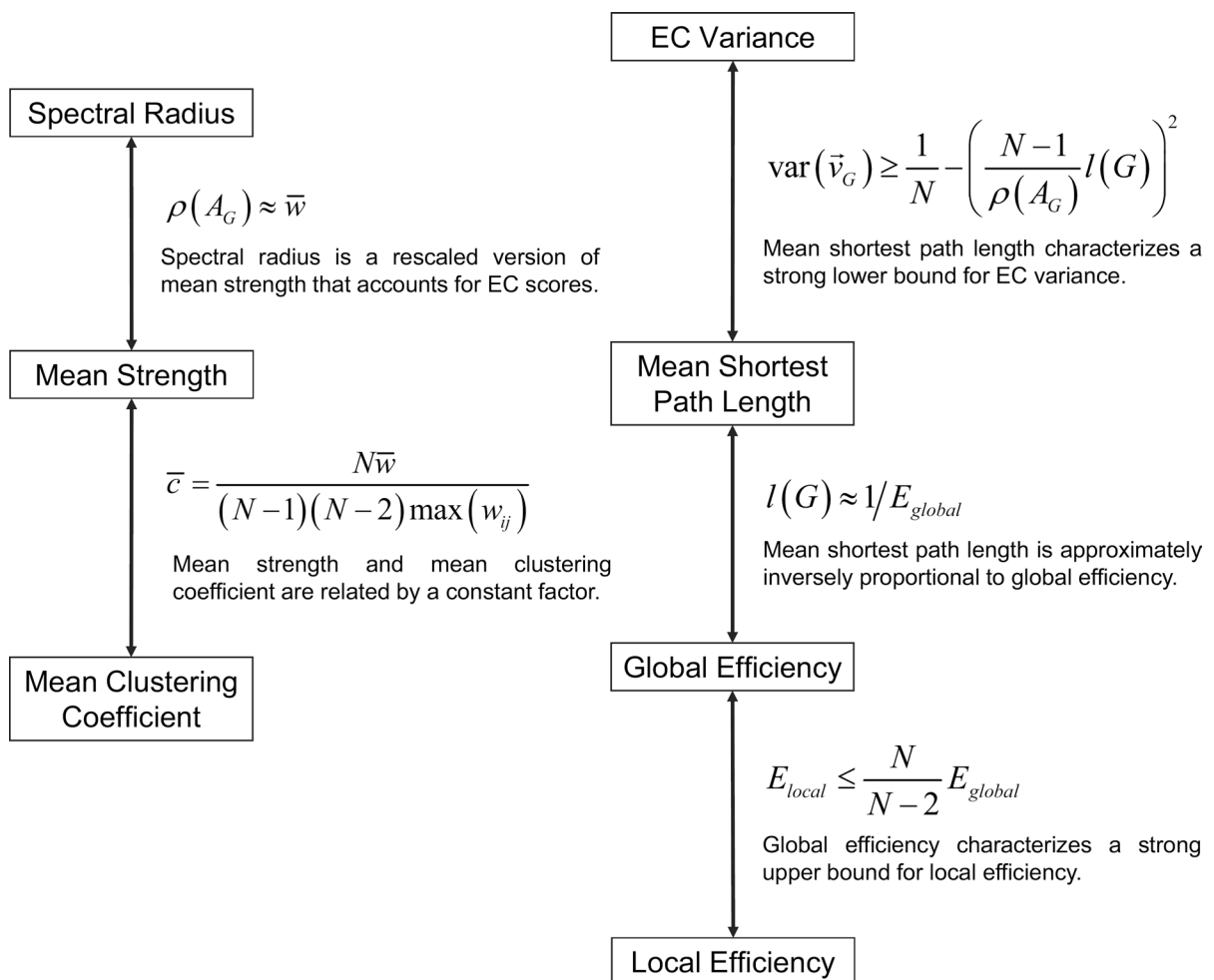
Spectral Radius

$$\rho\left(A_G\right) \approx \overline{w}$$

Spectral radius is a rescaled version of mean strength that accounts for EC scores.

Mean Strength

$$\overline{c} = \frac{N\overline{w}}{\left(N-1\right)\left(N-2\right)\max\left(w_{ij}\right)}$$

Mean strength and mean clustering coefficient are related by a constant factor.

Mean Clustering Coefficient

EC Variance

$$\mathrm{var}\left(\vec{v}_G\right) \geq \frac{1}{N} - \left(\frac{N-1}{\rho\left(A_G\right)}l(G)\right)^2$$

Mean shortest path length characterizes a strong lower bound for EC variance.

Mean Shortest Path Length

$$l\left(G\right) \approx 1/E_{global}$$

Mean shortest path length is approximately inversely proportional to global efficiency.

Global Efficiency

$$E_{local} \leq \frac{N}{N-2}E_{global}$$

Global efficiency characterizes a strong upper bound for local efficiency.

Local Efficiency

Fig. 2 Relating eigenmetrics to other popular network metrics. Note that many of the above relationships arise from the fact that adjacency matrices considered in this study are fully connected, zero-diagonal, nonnegative and symmetric. For details of their derivation, see Supplemental Material B. Correlations between metrics are presented in Table 1. Network metric abbreviations are given by: $\overline{w}$ = mean strength, E_{glob} = global efficiency, $l(G)$ = mean shortest path length, E_{loc} = mean local efficiency, $\overline{c}$ = mean clustering coefficient

Table 1 Correlation between eigenmetrics and other popular network metrics

	λ_G	$var(\vec{v}_G)$	$var(\vec{v}_G)$	$skew(\vec{v}_G)$	$\bar{w}$	E_{glob}	$l(G)$	E_{loc}	$\bar{c}$
λ_G	1.00								
$avg(\vec{v}_G)$	0.68	1.00							
$var(\vec{v}_G)$	−0.67	−0.99	1.00						
$skew(\vec{v}_G)$	−0.75	−0.47	0.46	1.00					
$\bar{w}$	0.98	0.80	−0.80	−0.74	1.00				
E_{glob}	−0.71	−0.90	0.90	0.52	−0.82	1.00			
$l(G)$	0.72	0.92	−0.92	−0.40	0.82	−0.94	1.00		
E_{loc}	−0.74	−0.90	0.90	0.57	−0.84	0.99	−0.93	1.00	
$\bar{c}$	0.97	0.82	−0.82	−0.76	0.99	−0.85	0.83	−0.87	1.00

[*]All Spearman coefficients are significant at the 5% confidence level. Correlations were calculated from adjacency matrices used in the agent-based model (see the main text). Analytically-derived relationships between eigenmetrics can be seen in Fig. 2 and Supplemental Material B. Network metrics are abbreviated as: $avg(\vec{v}_G)$ = mean of the eigenvector centrality, $\bar{w}$ = mean strength, E_{glob} = global efficiency, $l(G)$ = mean shortest path length, E_{loc} = mean local efficiency, $\bar{c}$ = mean clustering coefficient

highly correlated to spectral radius, e.g., mean shortest path length, global efficiency, and local efficiency (Table 1; Supplemental Material B). This supports the notion that our approach extends to other network metrics, avoids redundancy, and is useful for organizing information from a large set of available summary indices.

Agent-based model design

We illustrate the nested nature of network metrics using an example from ecology. In this discipline, a common use of network analysis is the measurement of habitat connectivity for species conservation (Urban and Keitt, 2001; Dixon et al., 2006). We use a metapopulation model of animal movement on a physical landscape to limit the variability of network structure and illustrate our approach.

In a network formulation, nodes represent habitat patches and edges represent corridors that facilitate individual dispersal. A desirable feature of a general approach is that it is robust to multiple outcomes. Therefore, we consider two ecological processes: spread and survival. Spread is measured as the time needed for an initial population on one randomly chosen node to occupy the last uninhabited node (i.e., time to full network occupation). Survival is measured as time to global extinction (i.e., no individuals are left on any patch). These two processes represent important objectives for species

conservation programs: the spread and dispersal of the target species, which makes their global population more resistant to collapse (Gotelli, 1995; Hanski, 1999), and supports the long-term persistence of the species population *à la* population viability analysis (Beissinger and Westphal, 1998; Morris and Doak, 2002).

The data are drawn from agent-based representations of single-species habitat networks. In the absence of extensive data on the ecology of species and interactions with the landscape, model simulation is a useful tool for analyzing the ecological implications of landscape structure (Urban et al., 2009; Moilanen, 2011; Rebaudo et al., 2013). The actions of the agents are probabilistic and provide a scenario where the predictive power of the chosen metrics is assessable amid stochastic population dynamics.

The ABMs are calibrated using data on prairie dogs (*Cynomys* spp.). Prairie dog conservation is a vital part of the conservation of the black-footed ferret, a critically endangered species in North America (USFWS, 2013). Indeed, black-footed ferrets are obligate predators, with prairie dogs making up over 90% of their diet (Sheets et al., ; Campbell et al., 1987). Prairie dog metapopulations can be represented as a network of multiple complexes consisting of multiple prairie dog families, with low-lying drainages, roadways and other landscape features serving as corridors (Roach et al., 2001). Distance is a dominating factor in successful prairie dog dispersal, supporting

the assumption of symmetry (Garrett and Franklin, 1988; Bevers et al., 1997; Holmes, 2008).

Building spatial networks of prairie dog complexes

First, we apply the algorithm as in Shanafelt et al. (2017) to build 6×6 adjacency matrices with predetermined spectral radius, EC variance, and EC skewness. The matrices represent 6 connected nodes, which is comparable to networks of prairie dog complexes (Antolin et al., 2006). ABMs of prairie dogs are simulated on these constructed networks. Lower and upper bounds of edge weights are consistent with the minimum and maximum distances between prairie dog complexes (Bevers et al., 1997; Holmes, 2008). We choose twenty spectral radii, spanning the spectrum of potential spectral radii in our system, to generate adjacency matrices. For each spectral radius we specify ten EC variance measures, and then repeat the process with eleven levels of EC skewness. After accounting for networks that have an EC variance of 0, there are 2200 networks configurations. Adjacency matrices were constructed in MatLab R2019b.

Prairie dog dynamics

We then construct an agent-based model of prairie dog dynamics, which includes births, deaths, and dispersal events, all of which are stochastic. Prairie dogs exhibit density-dependent growth (Garrett et al., 1982; Knowles, 1982; Hoogland et al., 1987; Reading, 1993; Miller et al., 1996), with evidence of a carrying capacity (Hoogland et al., 1987;

Johnson and Collinge, 2004; Holmes, 2008). At each time-step, a prairie dog on node i produces f_x offspring with probability,

$$1 - \exp\left[-r\left(1 - D_{x,i}\right)\right] \qquad (1)$$

where r is the intrinsic growth rate of prairie dogs and $D_{x,i}$ denotes prairie dog density on node i. It is computed as $D_{x,i} = x_i / K_i$, where x_i is the absolute number of prairie dogs and K_i represents prairie dog carrying capacity of node i. Prairie dog mortality on node i occurs with probability q_x.

Intraspecific competition influences prairie dog dispersal (Garrett and Franklin, 1988; Hof et al., 2002). We divide dispersal into the decision to disperse and the likelihood of successful dispersal (Amarasekare, 2004; Tang and Bennett, 2010), where prairie dogs disperse from node i with density-dependent probability

$$\begin{array}{ll} \frac{D_{x,i}}{D_{U,x}} & \text{if } D_{x,i} < D_{U,x} \\ 1 & \text{if } D_{x,i} \geq D_{U,x} \end{array} \qquad (2)$$

where $D_{U,x}$ is a fixed density threshold indicator. The decision to disperse is random but increasingly likely with higher prairie dog density. Above $D_{U,x}$, dispersal is certain.

After dispersing, the probability of successful arrival at another node is a function of distance and inversely related to the edge weight between two nodes (Hof et al., 2002). A dispersing animal completes a move from node i to node j if $Exp(M_x) > W_{ij}$. The term $Exp(M_x)$ represents a random variable drawn from an exponential distribution with mean M_x, which denotes the mean dispersal ability of

Table 2 Summary of parameters used in the agent-based model

Symbol	Description	Value
N_x	Initial number of prairie dogs on a patch	150
r	Prairie dog growth rate	0.74[a]
f_x	Prairie dog litter size	3[b]
q_x	Prairie dog mortality probability	0.575
$D_{U,x}$	Prairie dog density threshold affecting own dispersal	0.9[c]
M_x	Average dispersal distance of prairie dogs (km)	2[d]
K_i	Prairie dog carrying capacity on patch i	150

Approximated from: [a]Klebanoff et al. (1991), [b]Hoogland et al. (1987), [c]Salau et al. (2012), [d]Garrett and Franklin (1988). Parameters are compiled from several different regions and are intended to bound the parameter space rather than outline a specific case study

prairie dogs. The edge weight W_{ij} is the corridor distance between nodes i and j.

Table 2 provides a summary of agent attributes and parameters. Parameter values were calibrated from the empirical literature. In order to isolate the effects of network structure on model outcome, we assume that parameter values are homogenous across individuals and patches. A detailed description of the sequence of agent events for each ecological process is available in Supplemental Material C. Source code and simulation data can be found on the Open Science Framework (osf.io/5y7fu). ABMs were originally in NetLogo (Wilensky, 1999), but then were re-coded in MatLab 2019b. Finally, due the need to run a large number of simulations, the ABM was re-coded into R 3.6.2 and run on the MIGALE bioinformatics facility (https://doi.org/10.15454/1.5572390655343293E12). The agent-based model is applied to each network configuration, with 100 realizations per configuration for each ecological process (spread and survival).

Analysis of model outcomes

In order to test the capability of our approach to explain model outcomes, we first visually evaluate general trends in model outcome between and across network metrics. We then turn to regression models to investigate how different combinations of spectral radius, EC variance, and EC skewness perform as predictors of prairie dog spread and survival. Specifically, we regress median time to full network occupation (spread) and median time to single-species extinction (survival) on a set of network metrics as dependent variables. We conduct a full factorial experiment for each model outcome, using different combinations of each network metric individually, as well as their squared and interaction terms, as dependent variables. We use adjusted-R^2 and AIC model fit criteria to measure how much of the variation in the data is explained by the sets of network metrics. Each statistical metric is a widely-used criterion for evaluating model fit, and measuring both provides multiple perspectives of model fit while still penalizing additional parameters (in contrast to R^2, which increases with the number of parameters in the model).

Sensitivity analysis

Parameter choice can bias results from computational models and hamper general claims of statistical significance. ABMs are a boon in this regard because they allow for repeated scenario testing and targeted assessment of parameter effects in a controlled environment. Therefore, we perform sensitivity analysis on the population parameters of the prairie dog ABM and re-assess whether multi-metric regression models outperform single metric models. We give each default parameter value a ten percent increase/decrease, collect new simulation data, and document the change in adjusted-R^2 and AIC values for the regression models.

Results

Single metrics and ecological outcomes

Single metrics collapse networks and, more generally, systems, into a single dimension, allowing for coarse comparisons. Therefore, we investigate the relationships between single metrics and ecological scenarios in order to describe the relationship between network structure and model outcomes. In the next section we will compare results with single metrics to those which jointly consider multiple metrics (e.g., our nested moments approach).

We first focus on the relationship between network structure and spread. A high spectral radius represents low traversability across the network, which limits successful dispersal through the landscape (Fig. 3a). Spread is faster in networks with high EC variance because network structures with greater node heterogeneity contain a strongly connected node which, once inhabited, facilitates spread to all nodes (Fig. 3b). EC skewness does not have a clear relationship with spread (Fig. 3c).

A prominent working hypothesis in conservation is that connectivity is important for conservation. Indeed, this is the rationale for maintaining connectivity between habitat patches (Gilbert et al., 1998; Hanski, 1998; Dixon et al., 2006). Our simulations support this claim. Networks with low spectral radii coincide with greater survivability as measured by persistence time (Fig. 3d). Greater connectivity,
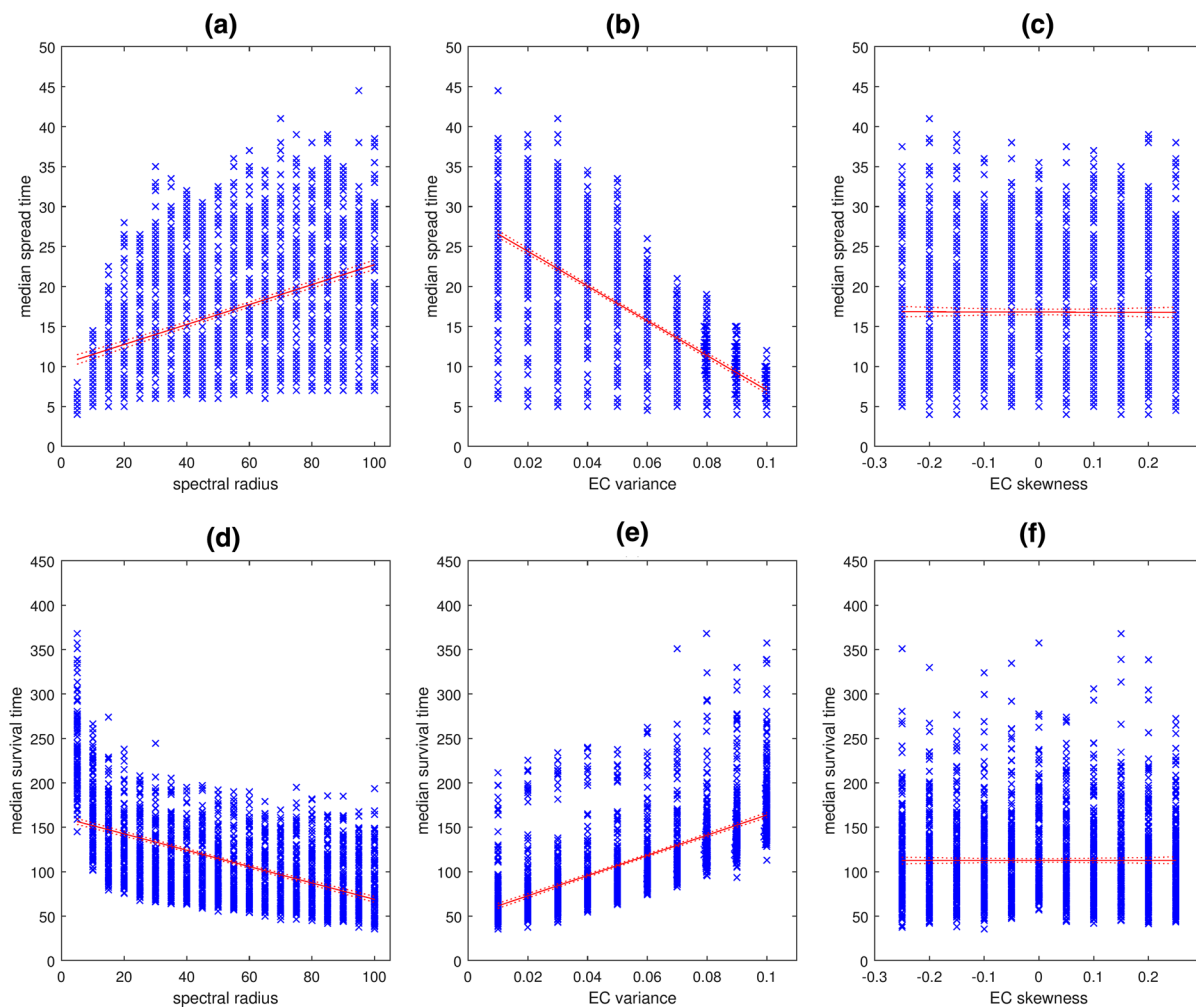
Fig. 3 Relating single indicators to ecological outcome. Each row pertains to the spread (**a–c**) and survival (**d–f**) scenarios. Data are presented as median measures of each model outcome. The solid red line in each plot represents a fitted linear trend in the data

indicated by lower spectral radius, allows greater mobility for foraging, securing refuge, and re-colonization. Networks with greater EC variance coincide with longer persistence times; in this case, the strongly connected node is the source of re-colonization and provides a rescue effect (Fig. 3e). As with spread, EC skewness does not have a clear relationship with survivability.

Grouping multiple metrics when evaluating model outcome

In contrast to looking at general trends in the data with respect to single network metrics, we now

evaluate the spread and survival results by jointly considering a system of metrics. We sort our results in the same order that the metrics are derived above. The sorting helps develop a narrative on how the combined effects of the metrics better elucidate the structure of the network and dictate model outcome. We highlight regions in the spread and survival scenarios when a single metric may be sufficient and ones where single metrics might tell an incomplete story. In doing so, it is useful to use qualitative terms such as "fast" or "slow" spread to describe regions in the space of model outcomes, or "low", "intermediate", or "high" values of a network metric to highlight areas of the network parameter space. We define them

arbitrarily with respect to our set of simulations; the exact values of the boundaries will change with the agent-based model parameters (for example, a region of fast spread or high survivability would shrink as the species growth rate is reduced). They are not meant to reflect actual prairie dog scenarios, but rather to help us relate properties of network structure to model outcomes.

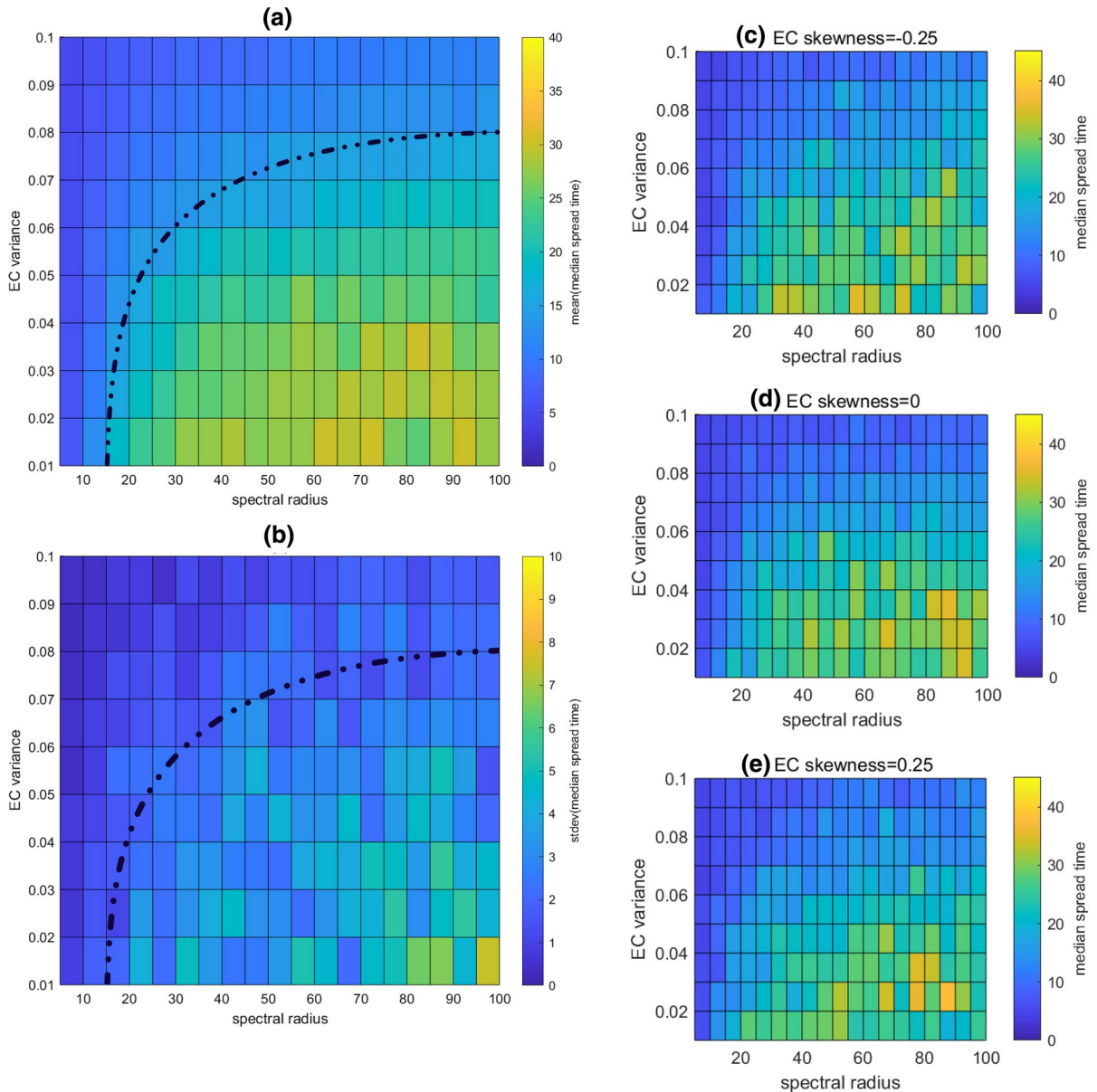In terms of *spread* outcomes, the key determinant of fast spread is node accessibility, where greater

Fig. 4 Grouping spread outcomes. In **a**, color denotes the median time to full network occupation, averaged across all values of EC skewness. Panels **c–e** present median spread times for select values of EC skewness. (Individual plots for all values of EC skewness can be found in Supplemental Material D.) Dark blue shades correspond to regions of fast spread; yel-low colors indicate regions of slow spread. In **b**, color denotes the standard deviation of spread time taken across all values of EC skewness. Dark blue shades indicate regions with lower variation across EC skewness; yellow colors correspond to regions of high variation. The dot-dashed line highlights the boundary between fast and more variable spread regions

node accessibility is indicated by low spectral radius and high EC variance (Fig. 4). Spectral radius is a sufficient indicator of fast spread in networks with a low spectral radius or high traversability ($\lambda_G \leq 15$ km) due to the overall closeness of nodes. In networks with a high spectral radius or low traversability ($\lambda_G > 40$ km), node heterogeneity becomes a deciding factor and a greater EC variance ($var(\vec{v}_G) \geq 0.08$) is related to faster spread times. We find that an intermediate traversability ($15 < \lambda_G \leq 40$ km) and intermediate EC variance ($0.06 \leq var(\vec{v}_G) < 0.08$) interact to increase spread time.

However, spectral radius and EC variance alone are unable to fully capture all spread scenarios (Fig. 4; Supplemental Material D). Traversability and node heterogeneity interact, with EC skewness providing additional information, to explain different patterns of spread outcomes. Take, for example, regions of intermediate traversability ($15 < \lambda_G \leq 40$ km), low node heterogeneity ($var(\vec{v}_G) < 0.06$), and positive proportion of strong to weak contributors ($skew(\vec{v}_G) > 0$) (Fig. 4; Supplemental Material D). When spread is slow, it is due to an extremely weak contributor in the network. Dispersing agents are unlikely to reach or escape the isolated node. This example illustrates the complexity of relating outcomes to specific network metrics, and highlights a key advantage of our approach.

In terms of *survival* outcomes, node accessibility and heterogeneity are also important for persistence (Fig. 5; Supplemental Material D). At intermediate to high levels of spectral radius ($\lambda_G \geq 20$ km) and low to intermediate levels of EC variance ($var(\vec{v}_G) < 0.08$), there exists a non-linear region of low survival. Network connectivity is sufficiently low to prevent re-colonization or support of extirpated or isolated nodes. However, we observe an increase in survival times at higher rates of EC variance ($var(\vec{v}_G) \geq 0.08$). Even in network configurations with overall low traversability ($\lambda_G \geq 40$ km), the presence of a strong contributor (a node highly connected to many others) is enough to lengthen the persistence time of the population.

Survival outcomes are more variable when spectral radius is low ($\lambda_G \leq 10$ km) (Fig. 5; Supplemental Material D). We would expect high traversability to help ensure survival, but other network properties play a significant role in determining survival time. Asymmetries in node contribution strength—a larger proportion of weak contributors (negative EC skewness) or strong contributors (positive EC skewness)—interact with the number of strong contributors and network traversability.

Take, for example, networks with high traversability ($\lambda_G \leq 10$ km) and positive EC skewness (Fig. 5e). Since there is a greater proportion of strong contributors to connectivity, EC variance is an indicator of the presence of weak contributors. When EC variance is low ($var(\vec{v}_G) \leq 0.05$), the system is full of strong contributors and survival time declines. If not replaced by individuals from other patches, immigrating individuals functionally act as additional mortality on an already stressed system. This is an example of a potential negative effect of dispersal. Increasing EC variance increases the number of isolated patches which, for survival time, stabilizes the system. While isolated patches do not receive immigrating individuals from other patches, their population remains under carrying capacity longer and faces less dispersal-related mortality.

In contrast, consider networks with high traversability ($\lambda_G \leq 10$ km) and negative EC skewness (Fig. 5c). While the network is overall well-connected (low spectral radius), there is a larger proportion of weak contributors (negative EC skewness). When EC variance is low ($var(\vec{v}_G) \leq 0.05$), nodes are more evenly (and weakly) contributing to connectivity, and survivability suffers. As EC variance increases, it implies more and more the presence of a strong contributor. Indeed, we observe increases in survival times with EC variance, which illustrates the positive effect of a strong contributor in the system.

For networks with low spectral radius ($\lambda_G \leq 10$ km) and zero EC skewness (indicating an equal number of weak and strong contribution nodes), the effects of each part of the network structure on survivability are difficult to ascertain (Fig. 5b). Our results are likely due to a complex relationship in how skewness interacts with spectral radius and variance. In this case, studying higher moments may play an important role in determining the relationship between networks features and model outcomes.

Single vs. multiple metrics: a statistical test of significance

While we observe heterogeneities in model outcomes within single metrics, we now turn to regression models to more quantitatively measure the amount
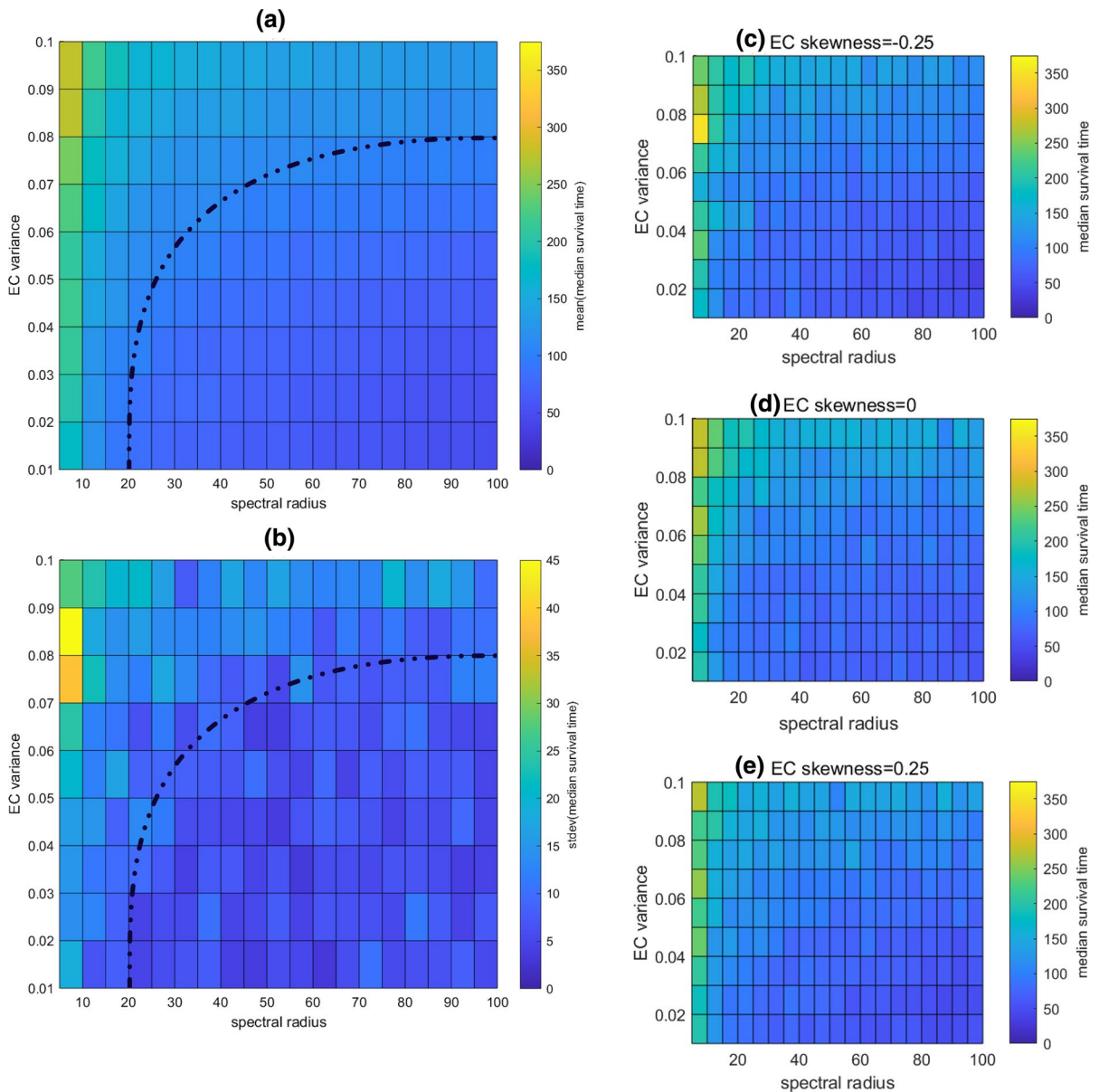
Fig. 5 Grouping survival outcomes. In **a**, color denotes the median time to full network *extinction*, averaged across all values of EC skewness. Panels **c–e** present median survival times for select values of EC skewness. (Individual plots for all values of EC skewness can be found in Supplemental Material D.) Dark blue shades correspond to regions of quick extinction; yellow colors indicate regions of longer persistence. In **b**, color denotes the standard deviation of survival time taken across all values of EC skewness. Dark blue shades indicate regions with lower variation across EC skewness; yellow colors correspond to regions of high variation. The dot-dashed line highlights the boundary between quick extinction and more variable survival regions

of variation in the spread/survival data that can be explained by network structure. Despite the general trends between single metrics and ecological outcomes reported in Fig. 3, a large degree of variation

in the simulated data remains unexplained when only considering a single metric (Figs. 4 and 5, Table 3).

The greatest amount of variation in both ecological scenarios is explained using multiple metrics,

Table 3 Assessing the best-fit model indicators of spread and survival

Ecological process	Network metric(s)			Adj-R^2	Δ AIC	Rank
Median spread time	λ_G			0.188	2631.550	6
		$var(\vec{v}_G)$		0.566	1251.776	3
			$skew(\vec{v}_G)$	0.000	3091.359	7
	λ_G	$var(\vec{v}_G)$		0.755	0	**1[f]**
	λ_G		$skew(\vec{v}_G)$	0.188	2633.516	5
		$var(\vec{v}_G)$	$skew(\vec{v}_G)$	0.566	1253.705	4
	λ_G	$var(\vec{v}_G)$	$skew(\vec{v}_G)$	0.755	1.875	2
Median survival time	λ_G			0.290	2106.463	3
		$var(\vec{v}_G)$		0.438	1593.612	5
			$skew(\vec{v}_G)$	0.000	2860.833	7
	λ_G	$var(\vec{v}_G)$		0.728	0	**1[g]**
	λ_G		$skew(\vec{v}_G)$	0.290	2108.453	4
		$var(\vec{v}_G)$	$skew(\vec{v}_G)$	0.437	1595.598	6
	λ_G	$var(\vec{v}_G)$	$skew(\vec{v}_G)$	0.727	1.970	2

Table of sample regression models using spectral radius (λ_G), EC variance ($var(\vec{v}_G)$), and EC skewness ($skew(\vec{v}_G)$) as predictor variables and median time values from the spread and survival scenarios as response variables. Adj-R^2 indicates the proportion of variability in outcomes explainable by a given model. AIC provides a measure of model fit that penalizes extra predictors; preferred models have lower AIC. Δ AIC is a rescaling of original AIC values by the lowest AIC value in the group of models. Original AIC value: [f]12455.623, [g]20538.166

even when penalizing models with extra predictors (Table 3). Some metrics do not explain much variation as single predictors but markedly influence fit when controlling for other metrics. Specifically, models pairing spectral radius and EC variance produce the greatest predictive power (or "best-fit") for either ecological outcome. According to adjusted-R^2 criteria, the model pairing spectral radius and EC variance is explains more-or-less the same amount of variation as a model with all three-network metrics. By

AIC criteria, the spectral radius-EC variance model is slightly preferred.

In general, network metrics can be decent predictors of spread, an unexpected result as we would predict a stronger relationship as landscape structure directly determines dispersal and indirectly influences persistence. However, including squared and interaction terms in the regression can greatly improve model fit (Table 4). Inclusion of a quadratic and interaction terms between spectral radius

Table 4 Best-fit models from a full-factorial regression analysis with interaction and squared terms

Ecological process	Network metrics	Adj-R^2	ΔAIC[†]
Spread	λ_G $var(\vec{v}_G)$ $\lambda_G \times var(\vec{v}_G)$ $\lambda_G \times skew(\vec{v}_G)$ $\lambda_G \times var(\vec{v}_G) \times skew(\vec{v}_G)$ λ_G^2 $var(\vec{v}_G)^2$ $skew(\vec{v}_G)^2$	0.833	–
	λ_G $var(\vec{v}_G)$ $\lambda_G \times var(\vec{v}_G)$ λ_G^2 $var(\vec{v}_G)^2$ $skew(\vec{v}_G)^2$	–	−840.261
Survival	λ_G $var(\vec{v}_G)$ $\lambda_G \times var(\vec{v}_G)$ λ_G^2 $var(\vec{v}_G)^2$ $skew(\vec{v}_G)^2$	0.850	–
	λ_G $var(\vec{v}_G)$ $\lambda_G \times var(\vec{v}_G)$ λ_G^2 $var(\vec{v}_G)^2$ $skew(\vec{v}_G)^2$	–	−1340.038

[†] Difference in AIC between the model presented here and the best-fit model reported in Table 3. A full-factorial design experiment that includes all combinations of each variable and their interaction and squared terms represents 1023 different model variations. Therefore, we only present the best-fit models here. Simulation data and code to generate all regression models can be found on the Open Science Framework (osf.io/5y7fu)

and EC variance/skewness improves the adjusted-R^2 to 83 and 85 percent in the spread and survival scenarios respectively, indicating that the overall distribution of connectivity of the network has important effects on species spread and survival.

Sensitivity analysis

Often in computation models, parameter choice can limit the ability to make general claims about model results. Therefore, we perform a sensitivity analysis on the prairie dog ABM parameters and re-assess whether multi-metric regression models outperform single metric models. A series of tables, one for each parameter perturbation, containing the adjusted statistical measures, can be found in Supplemental Material D.

For two parameter perturbations (increased prairie dog litter size and decreased mortality) in the survival scenario, extinction events became so rare that it was not possible to complete the necessary number of simulations to be included in our analysis. This is because reproduction and survival on any one node was sufficiently high to limit global extinction.

Though the ranking of single and two-metric regression models may change depending on parameter settings, we find that models with multiple metrics always provide the best indicators of spread and survival. In both spread and survival scenarios, regression performance is sensitive to prairie dog growth

rate and litter size parameters. In two experiments, the original adjusted-R^2 value reduced by almost a factor of 2 (Table 5). But even at the lowest adjusted-R^2 level, the 3-metric model remains a better predictor of survival than spread, which again is surprising given the presumed connection between network structure and dispersal. Perhaps this result is less astounding when one also considers the important linkage between dispersal and survival in the case of prairie dogs.

Discussion and conclusion

Network metrics and node centralities collapse the high dimensionality of networks into the measure of a single dimension, yet no single metric can precisely describe outcomes such as spread or survival in our model. Information is lost when considering only a single metric. Using multiple metrics in a systematic manner helps to retain structural information and describe different network attributes influencing model outcomes. In doing so, it is possible to negotiate tradeoffs between simple, readily interpretable metrics and the amount information lost through summarization of network properties.

Our systematic approach to network measurement begins at the global scale with the most general metric of structure (e.g., a single network metric), and then categorizes the network based on individual-scale

Table 5 Sensitivity of spread and survival results to parameter perturbation

Parameter	Perturbed value −10% (+ 10%)	Δ Adj-R^2 Spread	Survival
Initial number of prairie dogs on a patch, N_x	135 (165)[a]	0.017 (−0.001)	0.022 (−0.013)
Prairie dog growth rate, r	0.67 (0.82)	0.112 (−0.046)	−0.095 (0.305)
Prairie dog litter size, f_x	2 (4)[a]	−0.514 (0.053)	−0.064 (−)[b]
Prairie dog mortality probability, q_x	0.518 (0.633)	−0.047 (−0.320)	−(−0.065)[b]
Prairie dog density threshold, $D_{U,x}$	0.81 (0.99)	0.041 (0.039)	−0.001 (−0.012)
Average dispersal distance of prairie dogs, M_x	1.8 km (2.2 km)	−0.011 (0.003)	−0.016 (−0.002)
Carrying capacity, K_i	135 (165)[a]	0.013 (0.004)	−0.032 (0.037)

This table provides the quantitative change in adjusted-R^2 for the 3-metric linear regression model when perturbing model parameters. We systematically increase/decrease each default parameter by ten percent then recalculate the relationship between network metrics and outcomes. A positive Δ Adj-R^2 implies that the largest adjusted-R^2 associated with the perturbed model is greater than the largest adjusted-R^2 value reported in Table 3

[a] These values must be nonnegative integers

[b] We are unable to observe any meaningful relationship between metrics and median survival time because simulations with death rate 0.518 (and lower) or litter size 4 (and higher) seldom lead to extinction

heterogeneities (e.g., node centrality scores). We recover information in node centrality scores with routine formula for statistical moments. The mathematical dependence between the metrics determines the range of possible network configurations. With each network metric added to the hierarchy, we gain a clearer picture of network structure, which we can use to better understand model outcome.

In terms of evaluating spread and survivability by single metrics, we found that tradeoffs may exist between distinct structural properties. Traversability (measured by spectral radius) and node heterogeneity (measured by EC variance) strongly influence model outcome in opposite ways in each of our ecological scenarios. It is worth noting that this tradeoff exists because of the nature of the connection. In the context of a habitat network, the edge weight is interpreted as the distance between two nodes, and a higher value of spectral radius implies *less* connectivity. In a species interaction network, the weight would be interpreted as the strength of interaction between two species, and spectral radius would have the opposite interpretation (e.g., a higher value implies *higher* connectivity).

However, considering only one metric hides a more complicated relationship between network structure and model processes. Indeed, when we jointly consider multiple metrics, we uncover a complex story about the interactions between network properties and their effects on species spread and survival. Understanding and measuring multiple properties is likely important for conservation planning and requires multiple metrics. Ames et al. (2011) and May (2006) make a similar argument for disease dynamics on networks. Our findings hold across large regions of the agent-based model parameter space. This robustness is a key component in our assessment of network metrics on different of model outcomes. Tradeoffs in the accuracy and robustness of metrics are realistic, unavoidable, and amplify the hardships managers face when seeking to understand and influence dynamics on networks. Our approach, coupled with a controllable model, helps quantify these tradeoffs and inform the discussion on how to best summarize networks.

While our ecological example is for relatively small networks, we believe that our conclusions hold for larger networks and other study systems. We find similar patterns in analyses of bank failure (Nier et al., 2007; Gai and Kapadia, 2010; Haldane and May, 2011), disease spread (May, 2006; Ames et al.,

2011), habitat fragmentation (Thompson et al., 2017), and communication (Albert et al., 2000), although a formal consideration of the hierarchy is lacking. In each case, network properties beyond mean summary metrics matter in determining model outcome. For example, Nier et al. (2007) ($N=25$) and Gai and Kapadia (2010) ($N=1000$) evaluated the probability of bank failure given the topology of a banking network. While the overall connectivity of the network was important, modularity and clustering were both important factors in determining the propagation of shocks throughout the network. Ames et al. (2011) found differences in infectivity across contact networks with the same degree distribution but different mean paths and clustering coefficients ($N=10,000$). Thompson et al. (2017) iteratively removed nodes in a habitat network ($N=30$) to study the effects of habitat fragmentation on biodiversity and ecosystem functioning. They found that removing highly-connected "hubs" greatly degraded biodiversity and productivity compared to random removal—a phenomenon that also held in communication networks ($1000 \leq N \leq 20,000$) (Albert et al., 2000).

In order to isolate the effects of network structure on model outcome, we have assumed that model parameters are homogenous across individuals and patches. Relaxing these assumptions will affect spread and survival. Indeed, heterogeneities between habitat patches creating source-sink and rescue effects are well-established in the literature (Gotelli, 1995; Liebold et al., 2004; Loreau, 2010; Loreau et al., 2013), and have direct applications for species conservation (Harrison et al., 1988; Griffin and Mills, 2009; Russ and Alcala, 2011). These will interact with habitat network structure to shape the final spread or survival outcome. For example, using a patch-occupancy metapopulation model, Frank (2004) showed that heterogeneities in habitat patch size and dispersal linkages interact with species-specific parameters to determine the mean survival time of the overall metapopulation. This warrants future work. Similarly, our agent-based model is a simplified realization of a spatial metapopulation. In reality, prairie dogs face predation, environmental conditions, and disease (USFWS, 2013), many of which vary over space and time. While the model can accommodate some of this (by adjusting growth rates in our sensitivity analysis, for example), a more descriptive model may be needed if it is to be used

for a population viability analysis of a specific species (Morris and Doak, 2002).

As our study is theoretical in nature, it would be useful to validate our results with field data. However, doing so is a feat in and of itself. Dispersal experiments in the field can be difficult to conduct (Germain et al., 2017), and even in lab settings, obtaining the required number of networks and replicates is often infeasible given time, space, and budget constraints. Indeed, the last may be the greatest limitation. Such experiments are very costly, particularly if they need to be replicated. That being said, advances in meso- and microcosm experiments are a step in the right direction (Gilbert et al., 1998; Gonzalez et al., 1998; Srivastava et al., 2004; Legrand et al., 2012), with more recent work relating network structure and species dispersal to biodiversity, ecosystem functioning, and stability (Staddon et al., 2010; Thompson and Shurin, 2012; Gilarranz et al., 2017; O'Connor et al., 2020).

The interplay between grouped metrics highlights tradeoffs in structural design, which broadens the criteria for network selection. In general, the nature of the process and the layout of the edge weights determine the extent to which structural tradeoffs are feasible. In our ecological example, traversability is not the sole driving force behind long-term persistence and can be substituted by greater node heterogeneity. Structural tradeoffs also extend across multiple processes. We find that most networks promoting persistence also facilitate dispersal, but the converse is not true. Ordered multi-metric analyses do not provide a definitive summary of network dynamics, but help illustrate and understand the complexities in identifying preferred outcomes from network structures (e.g. structures that minimize invasive species spread, maximize survival, or a combination of both). Applying statistical moments does not create new metrics. Instead, it brings order to the large set of available networks metrics and facilitates combining them in a logical manner.

Declarations

Conflict of interests We have no competing interests to declare.

Ethics approval Not applicable.

Consent to participate Not applicable.

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