Quantifying the contribution of habitats and pathways to a spatially structured population facing environmental change

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Abstract

The consequences of environmental disturbance and management are difficult to quantify for spatially structured populations, because changes in one location carry through to other areas due to species movement. We develop a metric, G, for measuring the contribution of a habitat or pathway to network-wide population growth rate in the face of environmental change. This metric is different than other contribution metrics as it quantifies effects of modifying vital rates for habitats and pathways in perturbation experiments. Perturbation treatments may range from small degradation or enhancement to complete habitat or pathway removal. We demonstrate the metric using a simple metapopulation example and a case study of eastern monarch butterflies. For the monarch case study, the magnitude of environmental change influences ordering of node contribution. We find that habitats within which all individuals reside during one season are the most important to short-term network growth under complete-removal scenarios. Whereas the central breeding region contributes most to population growth over all but the strongest disturbances. The metric G provides for more efficient management interventions that proactively mitigate impacts of expected disturbances to spatially structured populations.

Introduction

Changes in the environment are altering ecosystems and landscapes (Barnosky et al. 2011; Krausmann et al. 2013) and affecting the size, distribution, and viability of wildlife populations (Kolbert 2014; Ripple et al. 2016). Migratory species present particular conservation and management challenges in changing environments (López-Hoffman et al. 2017). Because of their geographically distinct life cycles, abundance in one location may depend on environmental changes in far-removed areas. Many populations of migratory species are declining (Harris et al. 2009; Wilcove and Wikelski 2008), which diminishes the flow of ecosystem services they provide (Estes et al. 2011; López-Hoffman et al. 2017). Restoring these populations requires conservation actions for recovery and long-term persistence (Tucker et al. 2018; Visser et al. 2009; Wilcove and Wikelski 2008). Conversely, increasing populations can generate conflicts between stakeholders, for example from crop damages caused by herbivores (Buij et al. 2017; Skonhoft and Olaussen 2005; Zimmerman et al. 2019). All of these challenges arise at least in part from difficult-to-predict responses of migratory populations to environmental change and management actions.

A crucial need in developing effective management and conservation efforts for migratory species is assessing the relative importance of the habitats they occupy and move among over the course of their full annual cycle (Erickson et al. 2018; Hostetler et al. 2015; Wiederholt et al. 2018). In ecological modeling, multiple habitats (nodes) connected by migratory pathways (edges) make up a migratory network. Understanding how the levels of importance among habitats and pathways change under differing environmental conditions can aid decisions about where and when to allocate limited funds for habitat management. For example, if a manager has a fixed level of funding, are they better off enhancing the habitat in an overwinter location, breeding location, or one of the many possible migratory pathways?

Substantial theory exists for describing the importance of nodes and edges within networks (Barrat et al. 2004; Freeman 1978; Freeman et al. 1991; Opsahl et al. 2010). Although useful for static networks, these measures cannot accommodate seasonal variation in dynamics nor capture the effects of environmental change. Regarding dynamic environments, the per-capita contribution metric C^r quantifies the demographic contribution from a single individual at a node (i.e., through survival and reproduction) to an entire metapopulation (Runge et al. 2006). This metric is calculated over a fixed time interval and quantifies node importance to the dynamics of a population network during this timeframe. For predicting how a metapopulation will change due to a localized environmental pressure or management action, perturbation experiments have been used to quantify the effect of perturbing one, or more, of the habitats or pathways (Greene and Beechie 2004; Heppell et al. 2000; Ozgul et al. 2009). Change in metapopulation capacity was used to evaluate the impact of both small and large perturbations to patch size, including cases where habitats were completely removed or added (Ovaskainen and Hanski 2001, 2003). Other prospective analyses, such as sensitivity and elasticity, can be used to understand how demographic indices, such as population growth rate, respond to (small) changes in vital rates (Caswell 2001; Caswell and Shyu 2012; Hunter and Caswell 2005). In a metapopulation with two habitats of differing quality and undergoing environmental changes, elasticity of metapopulation growth rate depends on the distribution of individuals between habitats (Strasser et al. 2012). These findings have revealed consequences of localized environmental change for the viability of an entire metapopulation, where patches become habitable or uninhabitable over time.

In contrast with individuals in metapopulations, migratory animals exhibit seasonal, directed movements between nodes. These movements evolved as an adaptation to maximize fitness under seasonal fluctuations in habitat quality (Alerstam et al. 2003). Perturbation experiments are important for understanding how changes in size, quality, and existence of particular habitats affect population dynamics for migratory species. Earlier experiments ranged from theoretical models with very few parameters to complex individual-based models with many parameters. Building on work by Fretwell (1972), Sutherland (1996) used a 2-parameter model including density-dependent mortality and breeding output to predict effects of percentage losses of breeding and wintering habitat on the population size of a migratory species. Based on a single-parameter extension of this simple model, carry-over effects were found to exacerbate the effects of habitat loss (Norris 2005). More recently, studies have used diverse modeling approaches to quantify effects of habitat perturbations on changes in migratory population size. In increasing order of complexity, these include migratory network models (Taylor and Norris 2010; Wiederholt et al. 2013), deterministic population models (Mattsson et al. 2012; Robinson et al. 2016), stochastic projection matrices (Brown et al. 2017), migratory-flow-networks (Iwamura et al. 2013; Taylor et al. 2016), and integrated population models (Morrison et al. 2016; Oberhauser et al. 2017).

Although significant modeling advances have been made, still unknown is how the severity and type of perturbation can affect the ranking of importance among habitats. For example, Pettifor et al. (2000) showed removal of entire nodes vs removing the same amount of total area across a set of nodes had differing effects on population dynamics. We suspect habitat ranking may be highly sensitive to perturbation size for many species and network structures, but this result has yet to be investigated. When a focal habitat undergoes a mild perturbation, for instance, that habitat may be ranked as most important. By contrast, under severe perturbations (or habitat removal), the habitat ranking might change. Thus, a modeling framework and corresponding metrics are needed for comprehensive understanding of how changing localized environmental conditions will affect population dynamics for migratory species.

This paper develops a framework for assessing the consequences of environmental change in spatially structured populations. Specifically, we develop a metric to quantify the demographic contribution to network-wide population growth. The metric, G, is general and applicable to migratory and non-migratory species while allowing for populations with age or class structures. G assesses network sensitivity to localized environmental disturbance based on change in growth rate attributed to varying levels of enhancement or degradation of a given focal habitat or pathway. We define this contribution to network growth as the difference between the baseline network growth rate and the networks growth rate after a perturbation to a node or edge. In theory, network growth rate can be calculated over any length of time. However, since the model parameters will not be updated in response to the perturbation, we will measure the change in network growth rate in the short-term (over one annual cycle). A perturbation can be negative (degradation) or positive (enhancement). We allow for any magnitude of perturbation including complete removal. Importantly, we provide the framework and code for applying this metric to any spatially structured population.

We first develop the mathematical model for G and then illustrate its application with two case studies. Our first application uses the original source-sink model (Pulliam 1988) to illustrate the meaning and evaluate the usefulness of G in a straightforward example. Using the Pulliam model as a basis, we provide the mathematical construction of G and illustrate that the metric can be applied to a rather simple non-migratory spatially structured population. We then apply our model to the eastern migratory population of the monarch butterfly (*Danaus plexippus*). This case study demonstrates the metric for a stepping-stone migration and reveals the utility of G in identifying network connectivity issues. We show that the ranked importance among habitats or pathways can change with the magnitude of perturbation.

Generalized Model Development and Parameterization

To define G for a wide range of networks, we must first define a general representation for a spatially structured network. Symbols used throughout this paper are given in table 1. We consider a network in which habitats are nodes and movement pathways are edges (Sample et al. 2018; Taylor and Norris 2010). We consider a population of c classes (or life stages) in a network of n nodes and s seasons. Individuals are classified by both their class and location. Utilizing age- and size-structured matrix population models (Caswell 2001; Hunter and Caswell 2005; Pascarella and Horvitz 1998; Rogers 1966), we construct an $nc \times nc$ time-dependent projection matrix, $\mathbf{A}_t$, that contains both demographic (fecundity, class transition, and survival rates) and movement information (migration and survival probabilities). Matrix $\mathbf{A}_t$ projects the population, for all classes and nodes, from one time step to the next (from t to $t+1$), which represents one season in the annual cycle. Seasons may vary in length. One year, from t to $t+s$, is represented by s time steps. Details on how to construct $\mathbf{A}_t$ are found in Sample et al. (2019). The change in population projected over an entire annual cycle, beginning at any time t, is given by the seasonal product matrix,

$$\hat{\mathbf{A}}_t = \left(\prod_{\tau=t}^{t+s-1} \mathbf{A}_\tau^T \right)^T = \left(\mathbf{A}_t^T \mathbf{A}_{t+1}^T \cdots \mathbf{A}_{t+s-1}^T \right)^T = \mathbf{A}_{t+s-1} \cdots \mathbf{A}_{t+1} \mathbf{A}_t. \tag{1}$$

This matrix, and modifications to it, are used to calculate the contribution to network growth. It is important to note that $\mathbf{A}_t$ is formulated to apply demographic updates first followed by the dispersal of individuals in the network. Switching this order would modify $\mathbf{A}_t$ (Hunter and Caswell 2005) and consequently the matrices used to define the contribution metric.

The framework presented here can accommodate population models with density-dependent reproduction, survival, and movement probabilities. For example, if the demographic rates of the model are seasonal and density-dependent, then $\mathbf{A}_t$ might be modeled as a deterministic function of t and population sizes at time t, namely $\mathbf{A}_t \equiv \mathbf{A}\left(\vec{\mathbf{N}}_t, t\right)$ where $\vec{\mathbf{N}}_t$ is an $nc \times 1$ block vector whose $c \times 1$ subvectors $\vec{\mathbf{N}}_{i,t}$ give the class distribution within each node i at time t. Class-specific population sizes at each node can be iterated over time using the projection matrix, $\mathbf{A}_t$:

$$\vec{\mathbf{N}}_{t+1} = \mathbf{A}_t \vec{\mathbf{N}}_t, \tag{2}$$

Since $\mathbf{A}_t$ varies from one season to the next and $\hat{\mathbf{A}}_t$ varies from one annual cycle to the next, the contribution to network growth also has seasonal and annual variation. We call the season in which $\hat{\mathbf{A}}_t$ is calculated, the anniversary season.

Contribution to Network Growth

Habitat Metric

First, we define population proportion at time t as $\vec{\mathbf{w}}_t = \vec{\mathbf{N}}_t^T / N_t^{tot}$, where N_t^{tot} is the network population size (summed across all nodes and classes at time t). The annual growth rate of the network at time t is then calculated using the projection matrix of eq. (1),

$$\lambda_t = \frac{N_{t+s}^{tot}}{N_t^{tot}} = \vec{\mathbf{w}}_t \hat{\mathbf{A}}_t^T \vec{\mathbf{1}}_{nc} = \vec{\mathbf{w}}_t \left(\prod_{\tau=t}^{t+s-1} \mathbf{A}_\tau^T \right) \vec{\mathbf{1}}_{nc}, \tag{3}$$

where $\vec{\mathbf{1}}_{nc}$ is a $nc \times 1$ vector of ones. At equilibrium, $\lambda_t = 1$.

Next, we perturb the focal node r at time t by a fixed amount $\delta \geq -1$ during each season in the annual cycle and calculate the new annual network growth rate in the presence of this perturbation. We define the new network growth rate as $\gamma_{r,t}(\delta)$,

$$\gamma_{r,t}(\delta) = \vec{\mathbf{w}}_t \left(\prod_{\tau=t}^{t+s-1} \mathbf{D}_r(\delta) \mathbf{A}_\tau^T \right) \vec{\mathbf{1}}_{nc}. \tag{4}$$

The purpose of the matrix $\mathbf{D}_r(\delta) = \mathbf{I}_{nc} + \delta \sum_{x=rc-c+1}^{rc} \mathbf{E}_{nc,xx}$ is to alter the values of $\mathbf{A}_t$ that correspond to node r for every season in the annual cycle. Here, $\mathbf{I}_{nc}$ is the identity matrix of size $nc \times nc$ and $\mathbf{E}_{nc,xx}$ is an $nc \times nc$ zero matrix with a 1 at position xx. Complete node removal is represented by $\delta = -1$, hence $\mathbf{D}_r(-1)$ will zero out all entries corresponding to node r. In this paper, we use $*$ to indicate compete removal of a node or pathway. Thus, we define matrix $\mathbf{D}_r^* \equiv \mathbf{D}_r(-1)$ and the annual network growth rate in the absence of node r as $\gamma_{r,t}^* \equiv \gamma_{r,t}(-1)$. We note that in our formulation, individuals do not adapt to the habitat perturbation, because transition probabilities and demographic rates outside of the focal node are not changed in response to the perturbation. See Online Supplement S1 for a conceptual diagram of how the γ-metric is calculated.

Finally, we define the contribution to network growth of node r at time t as the absolute difference between the observed network growth rate (eq. (3)) and the network growth rate when the node is under the perturbation (eq. (4)):

$$G_{r,t}(\delta) = \left| \lambda_t - \gamma_{r,t}(\delta) \right|. \tag{5}$$

This metric represents the change in the network growth rate that is attributed to changes at node r. For the case of complete node removal, $\delta = -1$, we define the change in the network growth rate when node r is removed from the network as $G_{r,t}^* \equiv G_{r,t}(-1)$. Values of $G_{r,t}^*$ range from 0 to

λ_t. If $G^*_{r,t} = \lambda_t$, every individual must pass through node r at least once during its annual cycle and the population would go extinct (assuming no other behavioral changes) if that node is no longer in the network. If $G^*_{r,t} = 0$, then the node is unoccupied throughout the annual cycle and the population does not at all depend on the presence of node r. At equilibrium, values of $G^*_{r,t}$ range from 0 to 1. When the quality of the node is degraded, $-1 < \delta < 0$, we expect $G_{r,t}(\delta)$ to be between 0 and λ_t. If $\delta = 0$, the system is not perturbed and $G_{r,t}(0) = 0$. If $\delta > 0$, the quality of the node is enhanced by the perturbation and it is possible for $G_{r,t}(\delta)$ to be larger than λ_t. It is also possible to augment δ to be time-dependent so that a change in node quality occurs only once (i.e., in one season) over the course of the annual cycle.

Even with a fixed δ, G takes on different values depending on the selected anniversary season. To calculate a single metric for each node in the network across one full annual cycle, we use a seasonal population weighted average,

$$\overline{G}_r(\delta) = \frac{\sum\limits_{\tau=t}^{t+s-1} N^{\text{tot}}_{\tau} G_{r,\tau}(\delta)}{\sum\limits_{\tau=t}^{t+s-1} N^{\text{tot}}_{\tau}}.$$

Seasons with larger population abundance at the focal node are weighted more.

To understand the meaning of δ, consider an example perturbation of $\delta = -0.2$. This represents a 20% reduction to the focal node's quality throughout the annual cycle. Here, quality broadly means the combined demographic properties of all sex and age/stage classes at the node. So, a perturbation of $\delta = -0.2$ means that there is a 20% reduction in the growth rate of the node. That is, the population at the node will decrease by 20% after individuals reproduce and survive but before they migrate (or remain residents). This reduction is applied at every time step of the annual cycle and to all classes. If there are no individuals at the node then the nodal growth rate remains zero. δ takes advantage of the mathematical equivalency between growth rate and population change over a unit time period. On the other hand, a one-to-one correspondence between growth rates and vital rates is not necessarily true. For instance, if the growth rate is defined as fecundity times survival, then the product (not the fecundity and survival rates independently) will decrease by 20%. As another example, $\delta = 0.1$ represents a 10% improvement to the quality of the focal node, which increases the population growth rate of the node by 10% during every season of the annual cycle. Although in theory δ can be as large as desired, such large perturbations may not be realistic. A large δ in a non-breeding habitat is akin to setting survival rates greater than 1. It is advised to verify that $1 + \delta$ amounts to a reasonable increase in demographic rates. Since G depends on the degradation/enhancement amount, node ranking under complete node removal, $\delta = -1$, may be different than the ranking under small perturbations, $|\delta| \ll 1$.

Pathway Metric

We develop an analogous metric for quantifying the contribution of an edge (pathway). This metric gives the absolute change in network growth rate when the focal edge is perturbed by the amount $\delta \geq -1$. We define $\gamma_{rd,t}(\delta)$ as the network growth rate of the population when directed edge rd (origin node r and destination node d) is removed, degraded or enhanced for one full annual cycle beginning at time t,

$$\gamma_{rd,t}(\delta) = \vec{\mathbf{w}}_t \left(\prod_{\tau=t}^{t+s-1} \mathbf{A}_\tau^T \circ (\mathbf{B}_{rd}(\delta) \otimes \mathbf{1}_c) \right) \vec{\mathbf{1}}_{nc}, \tag{6}$$

where $\circ$ indicates the Hadamard product, $\otimes$ is the Kronecker product, $\mathbf{1}_c$ is a $c \times c$ matrix of ones, $\mathbf{B}_{rd}(\delta) = \mathbf{1}_n + \delta \mathbf{E}_{n,rd}$, and $\mathbf{E}_{n,rd}$ is an $n \times n$ zero matrix with a 1 at position rd. The purpose of the $\mathbf{B}_{rd}(\delta)$ matrix is to augment the values of $\mathbf{A}_t$ that correspond to edge rd by an amount δ.

The contribution of edge rd to network growth at time t is defined as

$$G_{rd,t}(\delta) = \left| \lambda_t - \gamma_{rd,t}(\delta) \right|, \tag{7}$$

which measures the total amount of growth lost (or gained) when we degrade (or enhance) the direct migratory route between habitats, where node r is the origin and node d is the destination for any season. When pathway rd is completely removed from the network, the values of $G^*_{rd,t} \equiv G_{rd,t}(-1)$ range from 0 to λ_t. G values for focal nodes and edges both represent the absolute change in the annual network growth rate under a perturbation, and are therefore directly comparable.

Note that a self-loop in the network represents individuals who forgo movement and remain at a node in a given time step. It is therefore important to apply caution when comparing the contributions of "true" pathways to the contribution of a self-loop, which is not a pathway in an ecological sense. For instance, $G^{*}_{rr,t}$ is the change in network growth rate when the self-loop rr is removed. Any individual who stays at node r for at least one time step would die, whereas any individual who migrates to or from node r would not be affected by the perturbation. In contrast, $G^{*}_{rd,t}$ is the change in network growth rate when the pathway rd is removed, which means that any individual who travels along edge rd for at least one time step would die.

Case Studies

In this section, we show how G is calculated for populations with contrasting life histories, movement patterns, and carrying capacities. In particular, we apply our model to a metapopulation and a stepping-stone migratory network. Here we present results for the habitat metric; pathway metric results are provided in Online Supplement S1. Code developed in R to calculate these metrics are available in an online repository (Bieri et al., 2019).

Pulliam Source-Sink Model

Pulliam (1988) developed a simple, theoretical, annual cycle model in a two-node network (figure 1*A*). He argued that a large, stable population in a sink node can be maintained by emigration from a smaller source node and cautioned that management decisions based on abundance could lead to unintended results.

In the spatially structured population of the Pulliam model, there is a small source node with high reproductive success but with a limited number of breeding sites. As the population grows toward equilibrium, the number of individuals in the node exceeds the number of breeding sites available, making the reproductive success density-dependent. Individuals who do not find a breeding site migrate to a lower quality node. This second node is a sink that hosts a large population with low reproductive success and large (unlimited) breeding area, meaning that all individuals are able to breed and do not migrate back to the source node. The annual cycle is modeled in a single time step, combining the breeding season, when there is no mortality, and the non-breeding season, when juveniles and adults survive with distinct probabilities. The two nodes do not differ in survival probabilities. Furthermore, population size is calculated by summing the number of adults and juveniles at the end of the annual cycle and therefore assumes that juveniles transition to adults at the end of every winter. This means that the population can be modeled with one class.

Here we translate Pulliam's model into our model notation. There are two nodes ($n = 2$), one season ($s = 1$), and one class ($c = 1$). Let $N_{1,t}$ and $N_{2,t}$ represent the number of individuals in the source, node 1, and the sink, node 2, at the beginning of year t's breeding season. Node 1 individuals who find a breeding site will remain residents with density-dependent probability $p_{11,t}$. Remaining individuals will move to node 2 with probability $p_{12,t} = 1 - p_{11,t}$. We define the per-capita growth contribution in year t of the source and sink as $\lambda_{1,t}$ and $\lambda_{2,t}$, respectively. By definition, a source has $\lambda_{1,t} > 1$ and a sink has $\lambda_{2,t} < 1$. System dynamics are governed by the following set of equations in which demographic updates at the nodes are applied first (summer reproduction then winter survival) followed by movement or residency in the spring (henceforth, movement update):

$$
\begin{aligned}
N_{1,t+1} &= p_{11,t}\lambda_{1,t}N_{1,t}, \\
N_{2,t+1} &= p_{12,t}\lambda_{1,t}N_{1,t} + \lambda_{2,t}N_{2,t}.
\end{aligned}
$$

This system of equations, which projects the population to the next year, can be written in the form of eq. (2), where the population at time t is $\vec{\mathbf{N}}_t = [N_{1,t}, N_{2,t}]^T$ and the population projection matrix of eq. (1) is

$$\hat{\mathbf{A}}_t = \begin{bmatrix} p_{11,t}\lambda_{1,t} & 0 \\ p_{12,t}\lambda_{1,t} & \lambda_{2,t} \end{bmatrix}. \tag{8}$$

The growth rate of the network (eq. (3)) is

$$\lambda_t = \vec{\mathbf{w}}_t \left(\prod_{\tau=t}^{t} \mathbf{A}_\tau^T \right) \vec{\mathbf{1}}_2 = \begin{bmatrix} w_{1,t} & w_{2,t} \end{bmatrix} \begin{bmatrix} p_{11,t}\lambda_{1,t} & p_{12,t}\lambda_{1,t} \\ 0 & \lambda_{2,t} \end{bmatrix} \begin{bmatrix} 1 \\ 1 \end{bmatrix} = \lambda_{1,t}w_{1,t} + \lambda_{2,t}w_{2,t} \tag{9}$$

where $p_{11,t} + p_{12,t} = 1$ and $w_{i,t} = N_{i,t}/(N_{1,t} + N_{2,t})$ is the proportion of the entire population in node i during year t.

Moving beyond Pulliam's analysis, we quantify the contribution of the source and sink nodes to network growth. We do so by enhancing/degrading the quality of the focal habitat and calculating the annual network growth rate in the presence of such a perturbation. This gives $\gamma_{r,t}$ of eq. (4) for node 1,

$$\begin{aligned} \gamma_{1,t}(\delta) &= \vec{\mathbf{w}}_t \left(\prod_{\tau=t}^{t} \mathbf{D}_1(\delta)\mathbf{A}_\tau^T \right) \vec{\mathbf{1}}_2 \\ &= \begin{bmatrix} w_{1,t} & w_{2,t} \end{bmatrix} \begin{bmatrix} 1+\delta & 0 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} p_{11,t}\lambda_{1,t} & p_{12,t}\lambda_{1,t} \\ 0 & \lambda_{2,t} \end{bmatrix} \begin{bmatrix} 1 \\ 1 \end{bmatrix} \\ &= (1+\delta)p_{11,t}\lambda_{1,t}w_{1,t} + (1+\delta)p_{12,t}\lambda_{1,t}w_{1,t} + \lambda_{2,t}w_{2,t} \\ &= (1+\delta)\lambda_{1,t}w_{1,t} + \lambda_{2,t}w_{2,t}, \end{aligned} \tag{10}$$

and for node 2,

$$\begin{aligned} \gamma_{2,t}(\delta) &= \vec{\mathbf{w}}_t \left(\prod_{\tau=t}^{t} \mathbf{D}_2(\delta)\mathbf{A}_\tau^T \right) \vec{\mathbf{1}}_2 \\ &= \begin{bmatrix} w_{1,t} & w_{2,t} \end{bmatrix} \begin{bmatrix} 1 & 0 \\ 0 & 1+\delta \end{bmatrix} \begin{bmatrix} p_{11,t}\lambda_{1,t} & p_{12,t}\lambda_{1,t} \\ 0 & \lambda_{2,t} \end{bmatrix} \begin{bmatrix} 1 \\ 1 \end{bmatrix} \\ &= p_{11,t}\lambda_{1,t}w_{1,t} + p_{12,t}\lambda_{1,t}w_{1,t} + (1+\delta)\lambda_{2,t}w_{2,t} \\ &= \lambda_{1,t}w_{1,t} + (1+\delta)\lambda_{2,t}w_{2,t}. \end{aligned} \tag{11}$$

Since the annual cycle is comprised of one season, only individuals beginning at the focal node will be “hit” by the perturbation. Any individual who begins at focal node 1, regardless if they choose to stay or move to node 2, will be affected by the perturbation, which explains the $(1+\delta)$ factor in eq. (10). If node 2 is the focal node, only individuals who begin at this node will be affected, hence the $(1+\delta)$ factor in the last term of eq. (11).

We now calculate the growth contributions (eq. (5)) of the source and sink nodes from eqs. (9) - (11),

$$G_{1,t}(\delta) = |\delta|\, \lambda_{1,t} w_{1,t},$$

$$G_{2,t}(\delta) = |\delta|\, \lambda_{2,t} w_{2,t}.$$

The growth contributions are plotted as a function of the perturbation amount δ in figure 1*B*, henceforth referred to as fountain graphs, for a chosen set of parameter values ($\lambda_1 = 1.05$, $\lambda_2 = 0.8$, $w_1 = 0.4$, $w_2 = 0.6$, and $p_{11} = 0.9524$). Under these conditions, we assume the source has reached the breeding site capacity, but the overall population is in decline because of poor conditions at the sink ($\lambda = 0.9$). The growth contribution of the sink ($G_2 = 0.48|\delta|$) is larger than the source ($G_1 = 0.42|\delta|$) for all values of δ since node 2 contributes a larger proportion of the population than node 1 ($\lambda_2 w_2 > \lambda_1 w_1$). This result implies that, for any given magnitude of δ, percent changes in the growth rate of the lower quality node would have a larger short-term impact on network growth rate than do equivalent changes to the higher quality node. It is possible under a different set of parameter values ($\lambda_2 w_2 < \lambda_1 w_1$) for percent changes in the growth rate of the higher quality node to have a larger short-term impact on network growth rate than equivalent changes to the lower quality node. Thus, it is possible for a node that hosts a minority of the population, provided its growth rate is large enough, to be ranked higher than a node with a larger proportion of the population. This supports Pulliam’s conclusion that caution should be taken when making decisions based on abundance. Note that G quantifies the growth contribution over one annual cycle; more work is needed to quantify the contribution of habitats to long-term population viability.

Monarch Butterfly

For a more realistic case study, we consider the eastern migratory population of monarch butterflies in eastern North America. Monarch butterflies complete a multi-generation migration over the course of the annual cycle. Individuals hatched in the northern U.S. and southern Canada migrate several thousand kilometers to wintering areas in the high-elevation oyamel fir (*Abies religiosa*) forests of central Mexico. Surviving individuals then, at the conclusion of winter, migrate into the southern U.S. to reproduce. Those hatched there migrate northward, following the advancement of spring and the availability of their breeding host plant, milkweed (*Asclepia* spp.). In the central and northern portions of the population's range, the species undergoes 2 - 3 more generations of reproduction, with the last generation making its return back to Mexico to begin the cycle anew.

Spatially explicit demographic models exist for the monarch butterfly (Flockhart et al. (2015); Oberhauser et al. (2017)). We converted the model developed by Flockhart et al. (2015) to a network-based model using the framework presented in Sample et al. (2018), comprising one sex and age class (adult females). An annual cycle consists of seven time steps or seasons: Winter, April, May, June, July, August, and September. The network contains four nodes representing regions of eastern North America: Mexico (M), South (S), Central (C), and North (N), and are enumerated 1 through 4, respectively. Mexico is considered a wintering node. The other three are breeding nodes, allowing for breeding each month. The seasonal-dependent network structure is shown in figure 2. The population is assumed to be at equilibrium. Edge transition and survival probabilities vary among seasons and are constant each year. Parameter values can be found in an online repository (Bieri et al., 2019).

The stepping-stone migration of monarchs indicates that the existence of Node 1 (Mexico) and Node 2 (South) are critical to the survival of the species, as removal of these nodes "breaks" the migratory network. The criticality of these nodes is apparent with G^* (table 2). Both nodes 1 and 2 have a growth contribution of $G^* = \lambda = 1$, which means that the absence of either node would eliminate the population. Node 3 (Central) is ranked as the third-most-important habitat in the network, and removal of this node reduces the average annual growth rate to nearly zero: $\overline{\gamma}_3^* = \lambda - \overline{G}_3^* = 0.0371$. Node 4 (North) contributes the least to network growth, and its removal reduces the average annual network growth rate to $\overline{\gamma}_4^* = \lambda - \overline{G}_4^* = 0.3551$.

The amount of perturbation strongly impacts the ranking of nodes (figure 3). For $-0.8 < \delta \leq -0.3$, node rankings are consistent; Node 3 (Central) and Node 2 (South) contribute the most to the short-term network growth rate, followed by Node 1 (Mexico) and Node 4 (North). As degradation becomes large and approaches complete node removal ($\delta \to -1$), Node 1 (Mexico), the only wintering node, becomes increasingly critical to the network growth rate. For a smaller degradation and any magnitude of reasonable enhancement ($-0.3 < \delta \leq 0.5$), Node 1 (Mexico) contributes the least to annual network growth rate. As an example, Node 3 (Central) would only need to be enhanced by $\delta \approx 0.07$ to increase network growth rate by 20% in the short-term ($G_3(0.07) \approx 0.2\lambda = 0.2$). By contrast, Node 1 would require an enhancement of $\delta = 0.2$ to achieve the same effect ($G_1(0.2) = 0.2$). We can also compare the effect of similar perturbation magnitudes on G. A 10% enhancement in the North results in about a 12% increase in short-term network growth rate ($G_4(0.1) \approx 0.12$), whereas a 10% degradation in the South results in about a 19% decrease in short-term network growth rate ($G_2(-0.1) \approx 0.19$).

Discussion

There are few places in the world unaffected by humans. Conservation of species in this human-altered environment, one which continues to change at a rapid pace, is difficult because the value of habitats to population dynamics is in constant flux. A habitat that little affects the dynamics of a species at present may become critical at some point in the future. We provide a metric, G, and associated computer code for predicting which habitats in a spatially structured population are most critical for short-term population viability. Further, we demonstrate how the approach is capable of revealing non-linear and unexpected changes in network growth rates under varying levels of environmental change and among discrete habitats and movement pathways.

A strength of G is that it can be calculated outside of equilibrium and measures the contribution of a habitat, or pathway, to the network growth rate in the short-term. In comparison, many other metrics require an equilibrium assumption. For example, U_i, for calculating the contribution of a patch to metapopulation size (Ovaskainen and Hanski 2003), is calculated at population equilibrium. Furthermore, G allows for both small and large perturbations. For large perturbation, U_i is the difference between the metapopulation size at equilibrium and the metapopulation size when patch i is removed, whereas G_i is the absolute change in the network growth rate when habitat i is removed or perturbed. Considering impacts of perturbations on network growth rate (instead of metapopulation size) allows for more refined comparisons among populations and environmental contexts.

While important information about migrating species can be gained from full perturbation experiments, these approaches are specific to the system to which they are applied and have important constraints on their application to new settings. In comparison, G is general and can be applied to any spatially structured population.

G clarifies important dynamics in realistic networks. For instance, nearly all levels of perturbation indicate that the Central breeding region for monarch butterflies contributes most to population growth. This finding is concordant with recent declines in this population, which dropped by 80% between 1993 and 2014 (Vidal and Rendon-Salinas 2014) due in part to the loss of milkweed in agricultural habitat of the midwestern U.S. (Pleasants and Oberhauser 2012, Flockhart et al. 2015, Thogmartin et al. 2017). However, if the overwintering area in Mexico were to undergo a similar degree of degradation, its importance to population growth would approach that of the Central breeding region, validating concerns about loss of overwintering habitat for this species (Oberhauser and Peterson 2003, Ramirez et al. 2015, Flores-Martínez et al. 2019).

Lemoine (2015) suggested that, under both moderate and severe emission scenarios and associated atmospheric warming, much of the South and Central regions will become less suited to monarchs, whereas the North is expected to expand in suitability. We find differential response to these perturbations when comparing degradation occurring in the South and enhancements in the North. Under the same magnitude of perturbation, the enhancement in the North results in an improvement that is smaller in magnitude than the decline experienced as a result of an equivalent degradation in the South. This could indicate that climate-induced changes that degrade the South might require a proportionally larger effort in the North to stabilize the population. However, it should be noted that G measures the effect of an isolated perturbation, one node at a time, and thus a true measure of the effect of mixed strategies would require a multi-perturbation approach. For example, with a northward range shift, southern migration success may decline, requiring mixed perturbations to both breeding nodes and the southern migration edges.

Calculating the contribution to network growth is useful for comparing sensitivity of population dynamics to consistent changes in conditions among habitats and pathways in a network. Habitats with a large proportion of the population may rank higher because they contribute more growth. In cases of habitat removal, unsurprisingly, we found that habitats through which all migrants flow are the most important to the network growth in the short-term. However, complete node removal is often not realistic in assessing the potential consequences of environmental change on population dynamics. Our formulation, therefore, allows for refined experiments that consider diverse perturbations including minor to severe degradation or enhancement. With this metric we can see how the ranking of nodes may depend on whether a habitat undergoes a small localized environmental change, a moderate shift in habitat quality, or complete removal of that habitat.

G gives information about a node that other metrics cannot. For example, Mexico provides the sole wintering habitat for the eastern population of monarchs. This single wintering node, where no reproduction occurs, would be considered a sink habitat in classic source-sink theory. It would also be deemed not as important when using the Sample et al. (2019) per-capita contribution metric C_r, which accounts for annual demographics and, like G_r, can compare breeding areas with non-breeding areas. In contrast, G_r clearly indicates overwintering sites in the high-elevation forests of central Mexico are vital to the short-term persistence of the population even if the reproductive value of the node is less than the other nodes. If this wintering node abruptly disappeared, the network growth rate would go to 0 resulting in the entire eastern population going extinct. On the other end, we found that habitat enhancement in the wintering areas in Mexico has the least ability to improve population growth in the short-term. Furthermore, habitats showed consistent rankings in their contributions to network growth under enhancement scenarios. Perturbation experiments on diverse network configurations are needed to evaluate whether this finding can be expected in other populations as well. At the same time, more work is needed to disentangle the mechanisms driving differential rankings among habitats under increasing degradation levels. To identify and mitigate the mechanisms inducing the decline of most migratory species, it is imperative to consider whether given the spatial structure, is the switch in importance between dominant breeding and nonbreeding nodes for large disturbances in migratory networks a general phenomenon?

The generalized formulation of G leads to a broad range of future directions for this work. An important area of research would be to investigate how habitat rankings change for populations far from equilibrium. For example, populations in decline may result in time-dependent reordering of habitat importance. The study of these types of transient dynamics could lead to important insights about the management of species undergoing large changes in population abundance. Additionally, the networks studied here were relatively small, whereas many species have a greater number of nodes and pathways to consider. Not only could parameterization of a very large network become cumbersome, but interpreting the results in a management context becomes complicated. This leads to an area of future research: investigating the true interpretation of metrics like G in the management context. What does habitat enhancement, a positive perturbation, mean in the management setting and what is its effectiveness for the preservation of species? Another avenue for future work is to extend the formulation of G to allow for simultaneous perturbations of nodes and pathways, which will allow for analysis of mixed strategies. If one habitat is degraded, what magnitude of enhancement at another habitat is required to stabilize network growth? What happens if a habitat and pathway are perturbed simultaneously?

More broadly, G_r needs to be compared to other approaches that rank the importance of habitats, such as the annual per-capita contribution metric C_r and full perturbation or agent-based approaches, to better understand the advantages and limitations of each approach. This comparison could include testing the sensitivity of these approaches to assumptions in the modeling process, understanding when similar approaches give equivalent or differing rankings, and investigating the utility of the metrics in deciding between viable management actions.

Understanding and predicting how populations change in the face of disturbance is a crucial step in mitigating negative consequences. As species adapt to changes in their environment, we can expect that new habitats may be colonized. To accommodate potential colonization, currently unoccupied habitats could be included in a network, providing no value at present and only becoming important to network growth as habitats are occupied. Allowing for the evolution of species behavior in response to habitat degradation is more complicated. An interesting area of future work would be expanding the formulation of G to allow network perturbations to affect movement and demographic rates.

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Table 1: Mathematical symbols used in the paper.

Mathematical Symbols

Symbol	Definition
$\otimes$	Kronecker matrix product
$\circ$	Hadamard (entrywise) matrix product
$*$	indication that the metric or matrix is evaluated at $\delta = -1$ (complete node or edge removal)
c	number of classes (life stages)
n	number of nodes (habitats) in the network
s	number of seasons in the annual cycle
t	time variable
N_t^{tot}	total network population size at time t
$\vec{\mathbf{N}}_t$	$nc \times 1$ block vector of population sizes of each node and class at time t
$\vec{\mathbf{w}}_t$	$1 \times nc$ vector of population proportion, $\vec{\mathbf{w}}_t = \vec{\mathbf{N}}_t^T / N_t^{tot}$
λ_t	annual growth rate of the network at time t, $\lambda_t = \vec{\mathbf{w}}_t \hat{\mathbf{A}}_t^T \vec{\mathbf{1}}_{nc}$
δ	perturbation amount for degradation $-1 \leq \delta < 0$ or enhancement $\delta > 0$
$\gamma_{r,t}(\delta)$	annual growth rate at time t when node r is perturbed by a factor of δ
$\gamma_{rd,t}(\delta)$	annual growth rate at time t when edge rd is perturbed by a factor of δ
$G_{r,t}(\delta)$	network growth contribution of node r at time t with perturbation δ, $G_{r,t}(\delta) = \lvert\lambda_t - \gamma_{r,t}(\delta)\rvert$
$\bar{G}_r(\delta)$	seasonal population weighted average of contribution to network growth for node r
$G_{rd,t}(\delta)$	network growth contribution of edge rd at time t with perturbation δ, $G_{rd,t}(\delta) = \lvert\lambda_t - \gamma_{rd,t}(\delta)\rvert$
$\mathbf{A}_t$	$nc \times nc$ projection matrix that contains demographic and movement rates at time t
$\hat{\mathbf{A}}_t$	$nc \times nc$ matrix that projects the population over an entire annual cycle, $\hat{\mathbf{A}}_t = \mathbf{A}_{t+s-1} \cdots \mathbf{A}_{t+1}\mathbf{A}_t$
$\mathbf{B}_{rd}(\delta)$	$n \times n$ matrix, $\mathbf{B}_{rd}(\delta) = \mathbf{1}_n + \delta \mathbf{E}_{n,rd}$
$\mathbf{D}_r(\delta)$	$nc \times nc$ matrix, $\mathbf{D}_r(\delta) = \mathbf{I}_{nc} + \delta \sum_{x=rc-c+1}^{rc} \mathbf{E}_{nc,xx}$
$\mathbf{E}_{n,rd}$	$n \times n$ matrix of zeros with a 1 at position rd
$\mathbf{I}_{nc}$	$nc \times nc$ identity matrix
$\mathbf{1}_n$	$n \times n$ matrix of ones
$\vec{\mathbf{1}}_{nc}$	$nc \times 1$ vector of ones

Table 2: Habitat contribution to network growth under complete removal.

Monarch Model

Metric		Winter	Apr	May	Jun	Jul	Aug	Sep	Seasonal Average
Node 1 (M)	$G^*_{1,t}$	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Node 2 (S)	$G^*_{2,t}$	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Node 3 (C)	$G^*_{3,t}$	0.9579	0.9579	0.9579	0.9567	0.9676	0.9733	0.9595	0.9629
Node 4 (N)	$G^*_{4,t}$	0.5938	0.5938	0.5938	0.5938	0.7225	0.7281	0.5936	0.6449

NOTE: Each column indicates the anniversary season for which the metrics were calculated. Metrics are for the case of complete habitat removal.

Figure legends

Figure 1: *A*, Two-node network diagram for the Pulliam (1988) metapopulation model. In this simple, one-season, one-class model, a portion of individuals in the source node move to the sink node. *B*, Fountain graph of the contribution to network growth, $\overline{G}_r(\delta)$, as a function of perturbation amount, δ, for the Pulliam model. Here, $\lambda_1 = 1.05$, $\lambda_2 = 0.8$, $w_1 = 0.4$, $w_2 = 0.6$, and $p_{11} = 0.9524$. The network is in decline ($\lambda = 0.9$) and the growth contributions for the source and sink nodes are $\overline{G}_1(\delta) = 0.42|\delta|$ and $\overline{G}_2(\delta) = 0.48|\delta|$, respectively. Note that the sink's contribution is larger than that of the source.

Figure 2: Network model for the monarch butterfly. Nodes that are occupied at the start of the focal season are colored.

Figure 3: Fountain graph for the seasonal-weighted average contribution to network growth, $\overline{G}_r(\delta)$ as a function of perturbation amount δ for monarchs. Legends identify the season in which nodes are occupied.