

Review

A management-oriented framework for selecting metrics used to assess habitat- and path-specific quality in spatially structured populations



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ABSTRACT

Mobile species with complex spatial dynamics can be difficult to manage because their population distributions vary across space and time, and because the consequences of managing particular habitats are uncertain when evaluated at the level of the entire population. Metrics to assess the importance of habitats and pathways connecting habitats in a network are necessary to guide a variety of management decisions. Given the many metrics developed for spatially structured models, it can be challenging to select the most appropriate one for a particular decision. To guide the management of spatially structured populations, we define three classes of metrics describing habitat and pathway quality based on their data requirements (graph-based, occupancy-based, and demographic-based metrics) and synthesize the ecological literature relating to these classes. Applying the first steps of a formal decision-making approach (problem framing, objectives, and management actions), we assess the utility of metrics for particular types of management decisions. Our framework can help managers with problem framing, choosing metrics of habitat and pathway quality, and to elucidate the data needs for a particular metric. Our goal is to help managers to narrow the range of suitable metrics for a management project, and aid in decision-making to make the best use of limited resources.

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1. Introduction

Spatial structure in populations occurs when a population occupies two or more distinct habitats that are connected by the regular movement of individuals. Spatial structure can be characterized in many ways, including classic metapopulations (Hanski, 1994), seasonal migratory systems (Mattsson et al., 2012; Nicol et al., 2015), nomadic systems (Dean, 2004) and even biophysical marine circulation systems (Cowen et al., 2006). Because movement links the dynamics between habitats, making decisions about how to effectively manage and conserve spatially structured populations poses enormous challenges (Skagen and Knopf, 1993; Kremen et al., 2007; Martin et al., 2007; Behrens et al., 2008; Miller, 2011). Further, species in spatially structured populations are often highly mobile, which can lead to social, economic, and political management challenges that cross multiple jurisdictions (Behrens et al., 2008; Semmens et al., 2011; Dallimer and Strange, 2015). In this context, managers need to decide where and when to take action to maximize the chances of meeting their objectives. Acting at the wrong time or place could result in misallocation of limited resources and lost opportunities to protect species (Martin et al., 2007; McCarthy et al., 2010). Uncertainty about the cause and effect relationships between management actions and objectives can also have unintended consequences—for example acting in one location may be offset by habitat losses, density dependence, or altered harvest quotas in another location (Sheehy et al., 2010; Runge et al., 2014).

One of the key questions for most decision makers interested in managing spatially structured populations is which habitat(s) or connections between habitats should be managed or protected to maximize the benefit to the population as a whole? This question is at the heart of decisions about how to allocate limited resources across space and time. Habitat-quality metrics, representing contributions of distinct habitats and the pathways which connect habitats to population dynamics, can be useful indicators to guide the allocation of conservation resources. However, the multitude of available metrics can make selecting an appropriate metric daunting. In a review of habitat-quality metrics within a metapopulation context, Runge et al. (2006) reported over 34 different metrics used to distinguish sources from sinks. Other studies have detailed a wide range of metrics to assess landscape connectivity (Urban and Keitt, 2001; Proulx et al., 2005; Urban et al., 2009), which is indirectly related to spatial population dynamics. Given the enormous range of metrics available for spatially structured models, how should a manager choose an appropriate metric or set of metrics to guide their decision making?

In this paper, we present a framework to help managers select a habitat- or pathway-specific quality metric based on the decision context of a spatially structured population. Our framework is based on common decision-making and management-planning frameworks including (structured decision making (Gregory et al., 2012); PrOACT (Hammond et al., 1999); and Open Standards for the Practice of Conservation (Conservation Measures Partnership,

2013)). We argue that metric selection depends on the management objective, the available management actions, and the data available. After introducing our framework, we illustrate how it can be used to select metrics in decision contexts involving common management objectives and actions from theory and practice. We do this by first reviewing objectives and actions found in the literature and then reviewing and classifying existing metrics into three classes based on their data requirements. We then identify suitable habitat-quality metrics for each management objective and action by using our metric classification scheme that is based on data requirements for objective-action combinations. Finally, we use our approach to make general observations about metric selection in spatially structured populations and to reveal knowledge gaps where new metrics may be needed.

2. Definitions and scope

We define habitats as distinct locations inhabited by part of all of a population during a given time period. Paths are dispersal or migration routes that connect habitats; individuals may pass along paths but do not spend much time there relative to time spent in habitats. A combination of habitats and paths forms a spatially structured population.

For the purposes of this study, we considered only habitat- and pathway-quality metrics for single-species population models. Although we acknowledge the importance of multi-species models, management objectives and actions are often species specific (Iwamura et al., 2013). We consider only metrics that can be used to evaluate individual habitat-specific and pathway-specific quality relative to a management objective, as opposed to metrics describing the response of whole networks or multiple habitats and pathways within a network (Moilanen and Hanski, 2001).

Our study reviews only those metrics which assume that the landscape used by a population is binary; that is, a given area is either habitat or non-habitat. This distinguishes our review from the broader study of landscape metrics, which accounts for landscape patterns in heterogeneous landscapes, but does not necessarily focus on habitat quality for any one species (e.g., Wu et al. (2002)).

Numerous studies review existing habitat-quality metrics (Tischendorf and Fahrig, 2000; Goodwin, 2003; Calabrese and Fagan, 2004; Kindlmann and Burel, 2008) but none link with decision theory to aid their use in management applications. Rather than providing a comprehensive review of all potential metrics that could be used for spatially structured populations, we provide an overview of categories of habitat- and pathway-quality metrics based on the relevant management objectives, management actions, and data requirements.

3. Methods

Our review consisted of four steps to answer the question “which metric should be used for a particular decision about managing habitats for a spatially structured population?”

First, we created a decision framework for metric selection based on management objectives, actions and data requirements. We used a theory of value-focused thinking for decision-making (Keeney and Gregory, 2005) to categorize metrics for management. Unlike previous reviews of metrics, which focus on classifying the metrics based on structural, disciplinary, or mathematical properties (Kindlmann and Burel, 2008; Rayfield et al., 2010), our approach used management objectives and potential actions to categorize metrics in terms of their suitability for management. Basing the selection of a quality metric on management objectives rather than on convenience or tradition helps to ensure that the metric will be appropriate for its intended use (Martin et al., 2007).

Second, we illustrated our framework by identifying a representative suite of management objectives and actions by reviewing the scientific literature and relevant government reports such as recovery plans. For each objective and action (we refer to the combination of an objective and action as an ‘objective-action pair’), we distinguished between objectives and actions used in practice and in modeling studies.

Third, because a key practical constraint on the usefulness of metrics is their data requirements (Calabrese and Fagan, 2004), we reviewed existing metrics and organized them into three classes based on the types of data required and the typical modeling approaches used with these data. In order of increasing data requirements, the three classes are: (1) graph-based metrics, predominantly drawn from graph theory, which require habitat locations and connectivity among the habitats (but do not require data on the presence or abundance of organisms); (2) occupancy-based metrics, many of which are based on metapopulation models, which require habitat-specific occupancy (i.e., presence or absence) data; and (3) demographic-based metrics, based on models of population dynamics, which require demographic parameters (survival, reproduction, transitions and/or movements) for each habitat and pathway in the network. Similar classifications have been used by previous reviews of habitat-quality metrics (e.g., Kindlmann and Burel (2008)).

After compiling and categorizing information from two disparate literatures (i.e., management objectives and actions, and available habitat- and pathway-quality metrics for spatially structured populations), the final step was to overlap these two literatures to determine which metrics can be used to solve the management problems identified in step 2, and the type of data required. We found relevant habitat-quality metrics for each objective-action pair identified in step 2 from the literature and then categorized each of these metrics by the minimum data required to calculate it using our three classes of metrics.

In this final stage, we were strict in our interpretation of valid metrics for each objective-action pair, and assumed metrics were relevant to a management objective only if they provided a direct measurement of the quantity specified by the management objective. For example, enhancing or preserving connectivity (one objective) by adding a habitat (management action) may increase persistence (another objective), but connectivity metrics do not measure persistence, and time-to-extinction estimates do not measure connectivity. Thus, we assumed that if enhancing persistence was the objective, then persistence should be specifically measured instead of assumed to increase as metrics related to other objectives (which may be correlated with persistence) also increased. This avoided the risk of failing to meet an objective because progress was measured using a proxy metric that does not directly represent the fundamental objective of management

(Keeney and Gregory, 2005). Using a proxy may be warranted in cases where the relationship between a proxy and an objective have been well demonstrated, but it is good practice to always examine the assumptions behind these proxies before using them.

4. Results

4.1. decision framework for selecting habitat-quality metrics

Our decision framework (Fig. 1) depicts the steps necessary to select a habitat quality metric for a spatially structured population. Defining management objectives and possible actions provides a basis for choosing a modeling framework and habitat- and pathway-quality metrics to guide management decisions (Fig. 1). After identifying an objective for the spatially structured population they are managing, managers can determine how to measure anticipated consequences of management actions in terms of this objective. Clearly defining their objectives and actions when managing a spatially structured population will help managers identify an appropriate habitat-quality metric and its associated data needs (Fig. 1).

Managers may decide additional data collection is required if existing data sets are not sufficient to compute an appropriate habitat-quality metric (Fig. 1). Because collecting data is costly, there is a tradeoff between using existing knowledge to make decisions with a less resource-intensive metric, versus collecting new data required for a more resource-intensive, but potentially more informative metric. Decision analytic tools can help identify which data are worth gathering to improve the expected management outcomes (Runge et al., 2011).

4.2. Reviewing management objective and actions

We identified eight broad categories of management objectives (Table 1) and four types of actions (Table 2) relevant to spatially structured populations. Six of the objectives were directly related to characteristics of the population, but two required additional information linking the population to another unknown (i.e., for climate change, information on the impact of climate scenarios on population parameters is required; for ecosystem services, a relationship linking the service to population size is required).

4.3. Classifying habitat-quality metrics based on data requirements

We classified existing metrics into three classes based on their data requirements. Here, we summarize each of the three categories and their associated quality metrics.

4.3.1. Graph-based metrics

Graph-theoretic models represent networks of habitats as a set of nodes (habitats) connected by edges (pathways) to represent some degree of connectivity (e.g., dispersal corridors or migratory paths). An appealing characteristic of graph-theoretic metrics is that they provide a method for estimating individual node and edge quality with very little data. Depending on how the nodes and edges are defined, many graph metrics can be defined with spatial data readily available from a map or geographic information system (e.g., habitat area and inter-habitat distance), but more sophisticated dispersal matrices can be defined if more data are available (Urban and Keitt, 2001). The minimum data requirements for a graph-theoretic metric are the locations and areas of the habitats and some information about the connectivity between habitats. While making decisions based on limited data is potentially risky, simple graph-theoretic metrics can provide a guide for where to direct further research and monitoring even in the

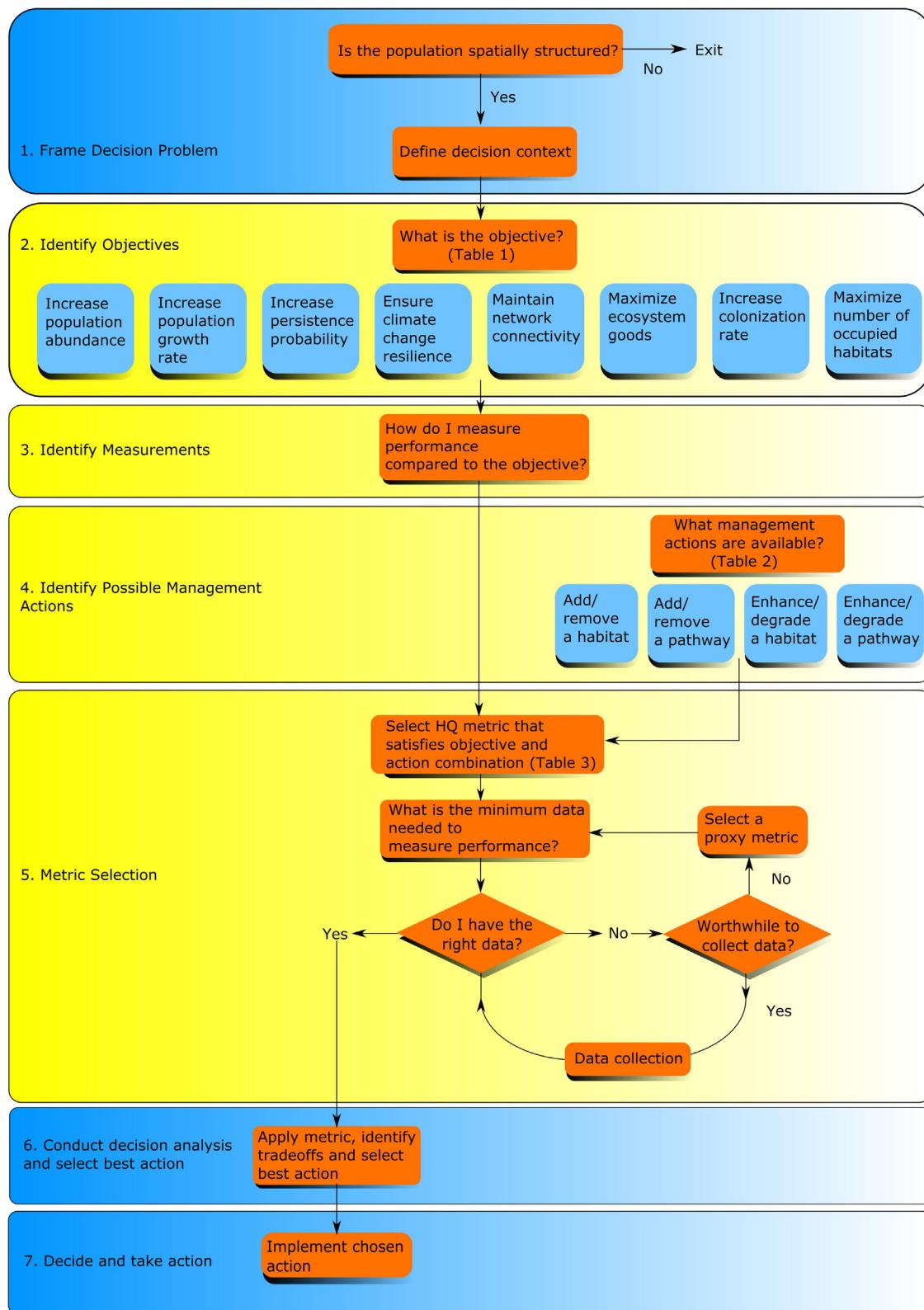


Fig. 1. Decision diagram for selecting a habitat quality (HQ) contribution metric for a spatially structured population as part of a formal decision making framework. Yellow boxes (i.e. steps 2–5) show the steps relevant to metric selection.

absence of sufficient data (Bunn et al., 2000; Urban and Keitt, 2001). When compared with more data-intensive methods, graph-theoretic metrics have been shown to perform well in identifying the most important habitat nodes using various selection criteria (Minor and Urban, 2007), although metrics that include a mea-

sure of habitat quality tend to out-perform simpler metrics (Wiens, 1989).

There are many graph metrics in use and they vary in complexity and what they target. A recent review identified over 60 metrics (Rayfield et al., 2010), which could be classified into four categories:

Table 1

Example management objectives, both applied (objectives that have been used in practice) and modeled (objectives obtained from the scientific literature that have not yet been implemented).

Management objective	Examples from recovery and management plans	Examples from published models (not yet implemented)
Increase population abundance	Monarch butterflies <i>Danaus plexippus</i> new Fish and Wildlife Service (USFWS) restoration goal (Office of Press Secretary, 2014) and federal conservation goal (Vilsack and McCarthy, 2015) Maintain a minimum of 1000 pairs of Kirtland's warbler <i>Setophaga kirtlandii</i> (Byelich et al., 1985) Cerulean warbler <i>Dendroica cerulea</i> conservation plan (Cerulean Warbler Technical Group, 2007)	Monarch butterflies (Flockhart et al., 2015) Chinook salmon <i>Oncorhynchus tshawytscha</i> (Greene and Beechie, 2004) Northern pintail <i>Anas acuta</i> (Mattsson et al., 2012)
Increase population growth rate	Monarch butterflies new USFWS restoration goal (Office of Press Secretary, 2014)	Bridled nailtail wallabies <i>Onychogalea fraenata</i> (Rout et al., 2009) Modeled per-capita contributions for metapopulations (Runge et al., 2006) Tasmanian devils <i>Sarcophilus harrisii</i> (McDonald-Madden et al., 2010) Mayflies <i>Callibaetis ferrugineus</i> and reef fish (Figueira and Crowder, 2006) Iberian lynx <i>Lynx pardinus</i> (Ferreras et al., 2001) Little bustard <i>Tetrax tetrax</i> (Bretagnolle and Inchausti, 2005) Little brown bat <i>Myotis lucifugus</i> and Indiana bat <i>Myotis sodalis</i> (Erickson et al., 2014) Samango monkeys <i>Cercopithecus mitis</i> (Swart and Lawes, 1996) Marine protected areas (McLeod et al., 2008)
Increase probability of persistence; maximize time to extinction	Peregrine falcon <i>Falco peregrinus</i> (Cade et al., 1988 ; Tordoff and Redig, 2001)	Waterfowl habitat (Nicol et al., 2014) 10 species of shorebirds (Iwamura et al., 2013) Wood thrush <i>Hylocichla mustelina</i> (Minor and Urban, 2007) Capercaillie <i>Tetrao urogallus</i> (Bodin and Saura, 2010)
Ensure climate change resilience*	Polar bear <i>Ursus maritimus</i> draft recovery plan (U.S. Fish and Wildlife, 2015)	Leisler's bat <i>Nyctalus leisleri</i> (Roscioni et al., 2014) North American waterfowl populations (Williams et al., 1996) Northern pintails (Mattsson et al., 2012) Eastern king prawns <i>Melicertus plebejus</i> (O'Callaghan and Gordon, 2008) Levins metapopulation model adapted to migratory populations (Taylor and Hall, 2012) Contribution to colonization for Glanville fritillary butterfly <i>Meitaea cinxia</i> (Ovaskainen and Hanski, 2003) Giant pandas <i>Ailuropoda melanoleuca</i> (Xu et al., 2006) Mexican spotted owls <i>Strix occidentalis lucida</i> (Urban and Keitt, 2001)
Maintain connectivity; maintain structure of network	Marine protected areas (Rudnick et al., 2012) Staying Connected in the Northern Appalachians, identification of critical movement areas for wildlife across U.S. and Canada (www.conservationregistry.org/projects/3837)	
Maximize ecosystem goods, e.g., sustainable harvest*	Northern pintail <i>Anas acuta</i> Harvest Strategy (U.S. Fish and Wildlife Service, 2010)	
Increase colonization rate	Metapopulation of black bears <i>Ursus americanus</i> in sky island habitats along Mexico-US border (Culver et al., 2009)	
Maximize number of occupied habitats	Tennessee purple coneflower <i>Echinacea tennesseensis</i> (Bowen, 2011)	

*Indicates that additional information linking the population to another unknown is required (i.e., for climate change, information on the impact of climate scenarios on population parameters is required; for ecosystem services, a relationship linking the provision of the service to population size is required).

route-specific flux (connectivity is based on source and destination strength and dispersal ability through the matrix); route redundancy (allows for multiple movement routes through the network); route vulnerability (quantifies the interactions and dependencies between routes to find key connections in the graph); and connected habitat area (the degree of effective connectivity from the perspective of specific organisms, so that habitats are based on their usefulness to the organism rather than purely on geometry). Many metrics within these categories measure similar characteristics, and while there may be some differences in the predictive ability of metrics under different circumstances ([Wu et al., 2002](#); [Pascual-Hortal and Saura, 2007](#); [Blazquez-Cabrera et al., 2014](#)), we

advocate choosing the simplest adequate metric that reflects the location, scale and objectives ([Rayfield et al., 2010](#)).

While we make the distinction here between graph-based metrics and metrics based on occupancy or demographic data (see below), it is important to note that some studies have used a hybrid approach by adopting graph theory terminology while using demographic-based models (e.g., [Taylor and Norris \(2010\)](#), [Wiederholt et al. \(2013\)](#), [Erickson et al. \(2014\)](#)). This hybrid approach borrows concepts from graph theory but uses demographic information to represent the dynamics of both nodes and edges. Combining approaches takes advantage of some of the analytical techniques of graph theory while using underlying demographic mechanisms to represent the dynamics of the system.

Table 2

Example management actions, both applied (actions that have been used in practice) and modeled (actions obtained from the scientific literature). Adding habitats and pathways can include reserve design or conservation planning cases when some intact lands are set aside while the remaining lands are transformed through time.

Action	Examples from recovery and management plans	Examples from published models (not yet implemented)
Add/remove a habitat	Corroboree frogs <i>Pseudophryne corroboree</i> and <i>P. penigilliei</i> (OEH NSW, 2012)	Elasticity and sensitivity analyses in matrix models (Caswell, 2001; Hunter and Caswell, 2005, Caswell and Shyu, 2012; Caswell, 2001; Hunter and Caswell, 2005, Caswell and Shyu, 2012).
Add/remove a pathway (movement path between habitats)	Western Swamp Tortoise <i>Pseudemydura umbrina</i> (Burbidge et al., 2010) Establishment of new routes for migratory Whooping cranes <i>Grus americana</i> (Urbanek et al., 2010)	Creation of new pathways: avian network model requiring site specific parameters (Taylor and Norris, 2010) Ratio of population decline/habitat loss (Sutherland, 1996, 1998)
Enhance/degrade a habitat	Western Swamp Tortoise wetland management <i>Pseudemydura umbrina</i> (Burbidge et al., 2010) Candidate restoration sites in Delaware Estuary for Black ducks <i>Anas rubripes</i> , Marsh Wrens <i>Cistothorus palustris</i> , and Least bitterns <i>Ixobrychus exilis</i> (Rudnick et al., 2012)	
Enhance/degrade a pathway	Migration management of Saiga antelope <i>Saiga tatarica mongolica</i> (Berger et al., 2008) California's south coast missing linkages, conservation plans for 11 key linkages www.scwildlands.org	Network metrics such as flux, influx, outflux that measures amount of movement between habitats (Minor and Urban, 2007) Samango monkeys <i>C. mitis</i> (Swart and Lawes, 1996)

However, as we argue in the discussion, additional information is not always ideal for all situations.

4.3.2. Occupancy-based metrics

Although graph-based metrics are appealing because of their low data requirements, for some management objectives they could be misleading because they do not provide ecological information that pertains to the management context nor the dynamics within a habitat. One of the most basic, and easily collected, types of data that can be gathered from habitats is the presence or absence (i.e., occupancy) of a species. Many occupancy-based metrics have been developed using the metapopulation framework. Metapopulations are assemblages of spatially delineated local populations, coupled by some degree of movement between populations (Hanski and Gaggiotti, 2004). The metapopulation concept assumes habitats undergo a dynamic process of colonization and extinction.

Although simpler measures exist (e.g., nearest neighbor distance), the most commonly used metrics for metapopulation habitat connectivity are derived from the incidence function model (Hanski, 1994). In the incidence function model, habitat connectivity is a function of habitat area and a dispersal kernel relating inter-habitat distance to the migration rate (Moilanen and Hanski, 2001). This model is used to create a Markovian transition matrix that describes the dynamics of the metapopulation in discrete time as a function of the colonization and extinction probabilities of the habitats in the metapopulation. The leading eigenvalue of the transition matrix is termed the metapopulation capacity (Hanski and Ovaskainen, 2000), and can be used to determine whether the metapopulation will persist in the long term. Metapopulation capacity is sensitive to changes in both habitat area and configuration, and provides a summary metric of the impact of changes to a habitat network. Ovaskainen and Hanski (2003) suggest that the quality of a habitat can be measured in terms of its response to perturbations or its contribution to the long-term fate of the existing system. Using metapopulation capacity, they derived metrics for a habitat's contribution to metapopulation size (number and size of habitats in a metapopulation), colonization events over the long-term, and metapopulation persistence and time to extinction.

The incidence function model assumes a particular model format (i.e., distance-based dispersal and area-based emigration) and can take many different forms depending on the data available (Etienne et al., 2004). However, the model assumptions may not be appropriate for some spatially structured populations. For example, there may be regional synchrony in population dynamics of some species, or colonization and extinction rates may vary over time (Ovaskainen, 2002). Models can be built that account for complexities not included in the basic incidence function model (e.g., disturbance and spatial autocorrelation between habitats (Frank and Wissel, 1998; Kallimanis et al., 2005); asymmetric connectivity (Bode et al., 2008); or the impact of the matrix on dispersal (Watts and Handley, 2010)).

4.3.3. Demographic-based metrics

In situations where the conservation objective requires understanding the impact of a management action on population size or growth rate, rather than on occupancy or connectivity, it is necessary to develop a model that includes demographic parameters (survival, reproduction, movement probabilities) for each habitat and pathway in the network.

We differentiated between two types of demographic-based metrics: perturbation metrics and 'snapshot' metrics. Perturbation metrics quantify the impacts of varying components of the network model associated with habitats or pathways on the population objective, whereas snapshot metrics evaluate the quality of habitats or pathways based on fixed attributes of the network that can represent a single point in time or equilibrium condition of the network.

4.3.3.1. Perturbation approach. A well-known approach to assess habitat-specific quality in a network with demographic data is to use perturbation analysis. Perturbation analysis involves small changes to vital rates to understand the influences of parameter change on population-level parameters such as population abundance or growth rates. Perturbation analyses are flexible and can accommodate complex population models including spatially explicit population models, optimal annual routine models, and individual-based models. The impacts of perturbations of vital rates on the population growth rate can be analyzed using sensitivity

and elasticity analyses (Caswell, 2001; Greene and Beechie, 2004; Hunter and Caswell, 2005; Caswell and Shyu, 2012). When the objective involves factors other than the population growth rate (such as population size, age structure, extinction risk or harvest levels), perturbation analyses are commonly applied to estimate the contribution of a particular habitat (Sutherland 1996, 1998; Pettifor et al., 2000; Caswell 2001; Hunter and Caswell, 2005; Fero et al., 2008; Taylor and Norris, 2010; Caswell and Shyu, 2012; Mattsson et al., 2012; Strasser et al., 2012; Bauer and Klaassen, 2013; Flockhart et al., 2015).

4.3.3.2. The ‘snapshot’ approach. Many snapshot demographic-based metrics are derived from source-sink theory. In a source habitat, birth and emigration rates exceed mortality and immigration rates; whereas in a sink habitat, mortality and immigration rates exceed birth and emigration rates (Pulliam, 1988). This approach identifies the per-capita contribution of a habitat or pathway by determining the number of individuals that an average individual contributes to the population in the next time step. Early metapopulation studies computed per-capita contributions using only the self-recruitment rate (survival and reproduction at time t without emigration or immigration) (Runge et al., 2006). More recent studies incorporate emigration and immigration as well as survival and reproductive rates of residents and emigrants; examples include C^r (Runge et al., 2006) and λ_c (Figueira and Crowder, 2006). Kroksek and Lewis, (2010) developed a similar per-capita metric to estimate the reproductive contribution of an individual; however, their metric is calculated using the number of adult progeny produced over the lifespan of an average individual at a location, rather than in one time step.

Comparing spatially segregated habitats based on local reproductive or recruitment metrics becomes problematic for migratory animals that have separate breeding and non-breeding habitats because non-breeding habitats are “sinks” with no reproductive output but with some mortality. However, non-breeding habitats are required for the viability of the network because individuals must use them for some part of the annual cycle. Thus, what is needed for a spatially structured population is a snapshot habitat-quality metric to account for the relative contributions of breeding and non-breeding habitats, as well as the pathways that connect these periods of the annual cycle.

4.4. Bringing it together: combining objectives, actions and data requirements

We present examples of metric selection in Table 3. Objectives are presented in the rows, and management actions in the columns. Suitable metrics are contained in the cells, which are colored to indicate the type of data required to calculate the relevant metric. For example, if a manager has an objective of increasing the probability of population persistence by adding habitat (row 2, column 1 of Table 3), then a suitable metric is the time to metapopulation extinction (Ovaskainen and Hanski, 2003), which can be calculated using occupancy data (orange colored cell; see caption for Table 3 for legend).

Most objectives that we reviewed required estimates of demographic parameters, which are the most data-intensive class of metrics (Table 3). The exceptions were objectives seeking to maintain connectivity in the network or to maintain occupancy, where less data are required for adding or enhancing habitats and pathways. Although the appropriate metrics varied when different management actions were considered, changing the management action did not change the class of data required for any of the objectives considered (Table 3).

For many objective-action categories in Table 3, multiple metrics in a class provided similar measurements. As such, within many

objective-action pairs, we presented a range of possible metrics. Quality metrics often differ in subtle ways that may be important for managers but are not captured by our objective-action framework. For example, graph degree and betweenness centrality both measure connectivity, but degree measures the number of neighbors connected to a habitat, while betweenness measures the frequency with which a habitat falls between other pairs of habitats in the network (Urban and Keitt, 2001). We suggest using the five criteria identified by Keeney and Gregory (2005) – unambiguous, comprehensive, direct, operational and understandable – when choosing among a set of metrics that match an objective-action pair.

5. Discussion

The number of metrics available for measuring the quality of a habitat or pathway in a network can be overwhelming for teams working to manage spatially structured populations. In this paper, we suggest managers define the decision context, objectives and the management actions they can implement to help select an appropriate metric. This classification scheme can help managers understand which class of metrics is best suited for particular decisions, narrows down the range of suitable metrics, and highlights whether additional data will be needed to predict management outcomes in terms of the objectives. Our decision-making process also illustrates whether a metric may be missing given the objective, management actions, and data availability; if metrics are missing, this gap can be used to guide future research efforts.

5.1. Data rich vs data poor metrics: when is a class of metrics appropriate?

Although some studies have listed the characteristics of good metrics within a single metric class (Pascual-Hortal and Saura, 2007; Saura and Pascual-Hortal, 2007), and others have found that metrics with lower data requirements can act as effective proxies for more data-rich objectives in specific studies (Minor and Urban, 2007), there have been no studies testing the different classes of metrics to provide rules about when to use a particular class of model. This may be because the appropriateness of a metric is context dependent (Etienne, 2004; Nicol and Possingham, 2010) so there may be no fixed rules; however, this remains an open question for future research. In this paper we have not settled this question, but we note some generalizations from our study.

Based on our study, the key management reasons for using more data-rich metrics include objectives requiring changes in abundance rather than presence or connectivity; providing resilience to climate change; providing ecosystem services such as a sustainable harvest; and more precisely timed management goals (Table 3, rows 5–8). For instance, increasing population size or growth requires more data than increasing likelihood of population persistence, so a demographic metric would be required rather than an occupancy metric for this objective. Similarly, goals aiming to provide benefits to humans (e.g., harvest) require more information than objectives that are purely species-based.

From the point of view of a decision maker faced with limited resources, the best metric may be one that captures the minimum amount of detail required to make a defensible decision (Martin et al., 2009; Nicol and Chadès, 2012). Consequently, management teams must consider the tradeoffs when choosing a more data-rich versus a more data-poor metric. Graph-based metrics quantify habitat quality using connectivity or network structure based on landscape configuration (Table 3). Their strength is that they rely on minimal data, but this means that many of these models rely on indirect or proxy measures of habitat suitability in lieu of demo-

Table 3

Habitat-quality metrics arranged by management objective (row) and management actions (columns). Cell colors indicate the minimum data requirements of the listed metrics in the cell. Light grey cells require graph-based data (e.g., distance and area); mid-grey cells require occupancy data; black cells require demographic data.

		Management Action			
Management Objective	Data requirement category	1. Add / remove habitat	2. Enhance / degrade habitat	3. Add / remove pathway	4. Enhance / degrade pathway
1. Maintain connectivity; maintain structure of network	Graph-based metrics	Degree, number of subgraphs, betweenness, diameter, traversability (Urban and Keitt 2001).	Quality-weighted area = patch size x patch quality (Minor and Urban 2007)	Degree, number of subgraphs, betweenness, diameter, traversability (Urban and Keitt 2001). Can also be calculated with demographic data, e.g., (Byelich et al. 1985)	Flux, influx, outflux = amount of movement between patches (Minor and Urban 2007)
2. Increase probability of persistence; maximize time to extinction	Occupancy-based metrics	Time to metapopulation extinction (Frank and Wissel 2002, Ovaskainen and Hanski 2003, Grimm and Wissel 2004)	Time to metapopulation extinction (Frank and Wissel 2002, Ovaskainen and Hanski 2003, Grimm and Wissel 2004). Can also be calculated with demographic data, e.g., (Byelich et al. 1985)		
3. Increase colonization rate	Occupancy-based metrics	Contribution to colonization events (Ovaskainen and Hanski 2003)	Contribution to colonization events (Ovaskainen and Hanski 2003) Can also be calculated with demographic data, e.g., (Rowland and Wisdom 2009)		
4. Maximize number of occupied habitats		Contribution to metapopulation size (Ovaskainen and Hanski 2003)			
5. Increase population abundance	Demographic-based metrics	Ratio of population decline/habitat loss (Sutherland 1996, Sutherland 1998, Taylor and Norris 2010) $C^r \times N$ (Runge et al. 2006), $\lambda_c \times N$ (Figueira and Crowder 2006)	Network model requiring demographic parameters (Taylor and Norris 2010) $C^r \times N$ (Runge et al. 2006)		
6. Increase population growth rate	Demographic-based metrics	λ_i : habitat-specific lambda, elasticity and sensitivity analyses, (Caswell 2001, Hunter and Caswell 2005, Caswell and Shyu 2012). C^r (Runge et al. 2006), λ_c (Figueira and Crowder 2006)	Elasticity and sensitivity analyses, (Caswell 2001, Hunter and Caswell 2005, Caswell and Shyu 2012). C^r (Runge et al. 2006)		
7. Ensure climate change resilience	Demographic-based metrics	Flyway capacity (graph theoretic but requires abundance) (Iwamura et al. 2013a)			
8. Maximize ecosystem goods, e.g., sustainable harvest	Demographic-based metrics		Perturbation analyses (Mattsson et al. 2012) (Greene and Beechie 2004)		Proportion of migrants reaching spawning grounds under harvest pressure (O'Callaghan and Gordon 2008)

graphics or occupancy. These models may therefore be inadequate if the management objective seeks to influence population size or persistence rather than population connectivity.

Occupancy models are suitable when the objective is species persistence—this may be relevant if the objective is to prevent extinction of an endangered species or eradicate an invasive species (Table 3, rows 2–4); however, if the abundance of the species within habitats is important, then demographic parameters may be required. Models requiring demographic parameters are necessary for several kinds of population objectives but their expensive data requirements may limit their use in many management applications. Note however that expert knowledge may provide a way to parameterize demographic models in the absence of empirical

data, for example in a Bayesian framework, although care needs to be taken to verify expert predictions (Martin et al., 2012).

Another reason to use a more data-rich metric depends on the ability of the species to respond to spatial and temporal variability. In the case of metrics using only network maps, inference is made on landscape characteristics without information on habitat patch quality or demographic information. For common species that are widely distributed and disperse easily, information on habitat patch quality may not be critical and network models may suffice, but as the requirements of the species become more specific it is likely that fine-grained (e.g., patch-level) data on habitat preferences of the species will become increasingly important (Ovaskainen and Hanski, 2003). For species that have large populations across multiple locations that are always occupied, an understanding

of population dynamics may be required (Nowicki et al., 2007). For these cases, teams managing spatially structured populations need to consider whether they are concerned with short-term fluctuations (environmental and/or demographic stochasticity), or whether understanding equilibrium dynamics will suffice.

5.2. Proxy metrics and the value of information

Most objectives require estimates of demographic parameters or occupancy (Table 3; rows 2–8). In practice, there are many management situations where occupancy data or vital rates are not available, and proxies will inevitably be used (Keeney and Gregory, 2005). In these situations, we still recommend using our objectives–actions framework to select a metric. This process encourages decision makers to make their objectives and possible actions explicit, which justifies why a proxy is selected or why additional data are required to measure the preferred habitat-quality metric. The tradeoffs that come with choosing a proxy metric can be debated and documented, ensuring that the limitations of the metric (and how what it measures differs from the objective) are well understood by managers.

In some cases it may be possible to collect necessary missing data, or to do a short study to verify that the proxy is adequate for the management circumstances. Expected value of information analyses can be used to quantify the benefits of obtaining additional information compared to acting under existing levels of uncertainty (Runge et al., 2011). When considering a proxy, the expected benefits resulting from the decision made with the preferred metric could be compared with the expected benefits of the decision made using the proxy metric. If the difference between these two values (i.e., the value of the information) exceeds the cost of collecting the information required for the preferred metric, then data collection should proceed. If not, then the proxy metric will suffice.

5.3. Scaling issues

Our review assumes that the landscape used by a population is separated into habitat and the surrounding matrix. Our tight focus on managing habitats for individual species in specific networks (in contrast to other studies that consider communities or changes in broad landscape patterns) means that there may not be a need to extrapolate across scales. In this context, given that the habitat network is defined and the assumptions understood, metric selection can proceed as outlined in this manuscript; however, care should be taken if comparing metric results with reference sites or other populations measured at different scales. The process of defining a habitat network is outside the scope of this review; however, here we provide a brief overview of some spatial and temporal scaling considerations relevant to habitat definition and management.

Scale depends on both the extent of the study (i.e., the overall area and the total duration of management) and the grain (i.e., the size of the management units and the duration between management events and/or population census) (Wiens, 1989; Wu et al., 2002). The extent of the study may affect the feasibility of objectives and management actions. For example, if the spatial extent is very large or the time horizon very long, management actions may be expensive to implement and objectives may be difficult to attain. Grain impacts the cost of management and the ability to observe population response to management, but its greatest impact is likely to be on habitat classification (Wiens, 1989). For many species, the definition of habitat may not be binary as species may use the matrix to varying extents. Defining patches requires selecting a threshold value to separate habitat from the surrounding matrix. Depending how the threshold is selected, small patches can be overlooked at large scales, and patches can be classified as too small or large if a use threshold is too strict or lax, respectively.

In both space and time, the appropriate scale will be influenced by the biology of the species being managed. Species with short colonization distances, small territories and rapidly changing life cycles may need to be managed at small spatial and temporal extent and high grain, and vice versa. The assumptions made to define habitats should be considered carefully to ensure that the objectives reflect the biology of the species being managed.

5.4. Knowledge gaps

Our framework to assist selection of habitat-quality metrics according to objective and management actions highlighted some knowledge gaps in the existing research (Table 3, rows 7 and 8). Of the metrics we reviewed, we found few linking habitat to objectives other than population-based characteristics, such as resilience to climate change or anthropogenic benefits from spatially structured populations (e.g., sustainable harvest). In these cases, additional information is needed to specify how habitat relates to these values, for example, via population sizes or other population-specific characteristics. When there is no suitable metric for an objective-action pair, managers currently need to either develop their own metrics or use proxies—these objective-action combinations are gaps for future research.

We also found that the majority of habitat-quality metrics we reviewed are focused on habitats rather than pathways. Most of the metrics that we discussed could be used to evaluate the quality of a pathway, but almost all metrics were measured at the habitat, and the quality of the pathway was obtained indirectly by observing the effect of the pathway on the habitat rather than the pathway itself. For example, the time-to-metapopulation extinction (Ovaskainen and Hanski, 2003) is a metric that can be used to evaluate the effect of altering a pathway by changing the connectivity strength between habitats; however, connectivity is parameterized using habitat occupancy observations – the cause of changes in connectivity must be inferred from observations at the habitat rather than the paths. The landscape ecology literature (Spiller et al., 1998; Kindlmann and Burel, 2008; Rowland and Wisdom, 2009) focuses much effort on understanding the composition and structure of the matrix, so metrics from this literature may be suitable to link management actions on paths to population objectives.

6. Conclusion

We described three classes of habitat-quality metrics available to decision makers faced with managing spatially structured populations. The three classes correspond with three distinct approaches to population modeling with increasing levels of data requirements. We also developed an objective-action framework to further classify habitat-quality metrics, which provides an important step toward narrowing the multitude of available metrics based on values-focused thinking. We found that the best metric depends on the management objective: graph-based metrics require the fewest data and may be suitable for objectives related to connectivity or structure; occupancy-based metrics may be suitable where the objective is species persistence; and demographic-based metrics are required where the objective includes abundance. The data required can constrain which metrics can be calculated, and managers need to consider whether further data collection is warranted to adequately measure progress towards the objective, or whether proxy metrics can be used to act now with existing information. Finally, we found that although there are many metrics that measure population objectives at the node, few metrics exist to measure pathway-based objectives or objectives that include values that are not solely population-based, such as resilience to climate change or anthropogenic benefits from spatially structured populations.

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