

Landscape complementation revealed through bipartite networks: an example with the Florida manatee

Catherine G. Haase · Robert J. Fletcher Jr. · Daniel H. Slone · James P. Reid · Susan M. Butler

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Abstract

Context Landscape complementation, or how landscapes that contain two or more non-substitutable and spatially separated resources facilitate resource use, is critical for many populations. Implicit to the problem of landscape complementation is the movement of individuals to access multiple resources. Conventional measures of complementation, such as habitat area or distance between habitats, do not consider the spatial

configuration of resources or how landscape features impede movement.

Objectives We advanced a bipartite network approach to capture the spatial configuration and connectivity of two habitat types and contrasted this framework to conventional approaches in a habitat selection model.

Methods Using satellite-telemetry of the Florida manatee (*Trichechus manatus latirostris*), a marine mammal that relies on two distinct, spatially separate habitats for foraging and thermoregulating, we parameterized and compared mixed conditional logistic models with covariates describing classic habitat selection metrics, conventional measures of landscape complementation, and bipartite network metrics.

Results The models best supported included habitat area, resistance distance between habitats, and the bipartite network metric eigenvector centrality. The connectivity between habitats and the spatial configuration of one habitat type relative to other types better described habitat selection than conventional measures of landscape complementation alone. The type of habitat, i.e. seagrass or thermal refuge, influenced both the direction and magnitude of the response.

Conclusions Landscape complementation is an important predictor of selection and thus classic complementation measures are not sufficient in describing the process. Formalization of complementation with bipartite network can therefore reveal effects potentially missed with conventional measures.

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C. G. Haase (✉)
School of Natural Resources and Environment, University of Florida, 103 Black Hall, PO Box 116455, Gainesville, FL 32611, USA
e-mail: cghaase@gmail.com

Present Address:
C. G. Haase
Department of Microbiology and Immunology, Montana State University, 109 Lewis Hall, PO Box 173520, Bozeman, MT 59717, USA

R. J. Fletcher Jr.
Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, PO Box 110430, Gainesville, FL 32611-0430, USA

D. H. Slone · J. P. Reid · S. M. Butler
U.S. Geological Survey Wetland and Aquatic Research Center, 7920 NW 71 Street, Gainesville, FL 32653, USA

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Introduction

Landscape complementation occurs when an organism requires two or more non-substitutable and spatially-separated resources located across landscapes (Dunning et al. 1992). Areas in which habitats are within close proximity are likely to support relatively high population densities as they allow for the exploitation of both resources with little energy required for traveling between habitats (Brotons et al. 2005; Haynes et al. 2007). Though originally introduced to describe population abundances in response to landscape-level processes (Dunning et al. 1992; Bianchi et al. 2006; Dulaurent et al. 2011), landscape complementation can also be considered a critical element in the process of habitat selection (Leopold 1933; Ouin et al. 2004; Miguet et al. 2013). The reliance of multiple, spatially-separated habitats can potentially constrain animals in their use or selection of habitat types during critical seasons or within different life-history stages (Kenagy et al. 2002; Choquenot and Ruscoe 2003).

Landscape complementation has been incorporated into resource selection models by recording the presence or proportion of complementary habitat within a specified buffer or by measuring the distance between habitat types (Choquenot and Ruscoe 2003; Ouin et al. 2004; Miguet et al. 2013; Smith et al. 2013; Table 1). These measures, however, do not consider the spatial arrangement of habitat patches (i.e. configuration) or how landscape features may impede movement (i.e. connectivity; Taylor et al. 1993). Though distance measures between complementary habitat patches describe their proximity, configuration extends beyond the patch-level and characterizes how clumped or isolated resources are in their entirety (Gustafson 1998). Furthermore, it is increasingly realized that distance measurements (e.g., Euclidean distance) may not accurately reflect effective distances between locations due to resistance of habitat features to animal movement. Distance measurements that incorporate landscape resistance can better quantify connectivity between habitats (McRae 2006; McRae

and Beier 2007), but resistance has yet to be incorporated into landscape complementation for describing proximity (Pope et al. 2000). By not examining configuration and connectivity, assessments of landscape complementation may be limited.

Both the compositional and configurational effects of landscape complementation can be captured through the use of network analysis. Spatial networks are derived from graph theory, where each patch is considered a node, and the links between nodes are described by potential or actual movement (Fig. 1; Urban and Keitt 2001; Fletcher et al. 2011, 2015). While network analysis is increasingly used to depict issues of landscape connectivity (Fletcher et al. 2016), it has not been considered as a means to capture landscape complementation, in part because of the challenge of considering the resources of two distinct habitat types. However, the concept of bipartite networks may fulfill this need. Bipartite networks are networks that contain two distinct sets of nodes that only link between sets and not within sets (Fig. 1b; Strogatz 2001; Albert and Barabasi 2002). By restricting a network as bipartite, we can quantify the proximity, connectivity, and configuration of two habitat types within a single metric, which may better capture the connectivity of the landscape, the dispersal capabilities of the organism, and the configuration of complementary habitats. Quantifying the spatial relationship between two habitats, rather than landscape patterns as a whole, specifically focuses on a critical mechanism that may ultimately dictate behavioral processes such as habitat selection.

Our objective was to extend the use of bipartite network analysis to capture landscape complementation and provide an application of this use. We contrasted this framework with conventional approaches for interpreting landscape complementation (Table 1) in habitat selection of the Florida manatee (*Trichechus manatus latirostris*), a species that requires distinct habitats that are often spatially separated. The Florida manatee is an herbivorous marine mammal that is distributed along the coast of the southeastern United States. Manatees forage in offshore seagrass beds and for freshwater submerged aquatic vegetation (Packard and Wetterqvist 1986), but in winter, often rely on critical thermal habitats located inland (Laist and Reynolds 2005a, b). We determined if the configuration and connectivity of habitats better explains selection over focal patch

Table 1 Research studies that have quantified landscape complementation, the quantification method, the animal process in question, and study species used

Reference	Animal response	Quantification method	Study species
Brotons et al. (2005)	Distribution	Presence within radius	Tawny pipit (<i>Anthus campestris</i>), skylark (<i>Alauda arvensis</i>), short-toed lark (<i>Calandrella brachydactyla</i>), and Calandra lark (<i>Melanocorypha calandra</i>)
Choquenot and Ruscoe (2003)	Population density	Euclidean distance ^a	Wild pigs (<i>Sus scrofa</i>)
Diekötter et al. (2010)	Species richness	Euclidean distance ^a	Ground beetles (Carabidae), spiders (Araneae), millipedes (Diplopoda), woodlice (Isopoda) and epedaphic springtails (entomobryid Collembola)
Dulaurent et al. (2011)	Individual survival	Presence within radius	Pine processionary moth (<i>Thaumetopoea pityocampa</i>)
Falke et al. (2013)	Distribution, Abundance	Presence within radius	Steelhead salmon (<i>Oncorhynchus mykiss</i>)
Haynes et al. (2007)	Population density	Area within radius	Red-legged grasshopper (<i>Melanoplus femurrubrum</i>)
Hocking and Semlitsch (2007)	Habitat selection	Euclidean distance ^a	Gray treefrog (<i>Hyla versicolor</i>)
Kamps et al. (2017)	Survival	Area within radius	Northern bobwhite quail (<i>Colinus virginianus</i>)
Le Pichon et al. (2006)	Distribution	Euclidean distance ^a	Common barbel (<i>Barbus barbus</i>)
Miguet et al. (2013)	Habitat selection	Area within radius	Eurasian skylark (<i>Alauda arvensis</i>)
Morellet et al. (2011)	Habitat selection	Area within radius	Roe deer (<i>Capreolus capreolus</i>)
Mueller et al. (2009)	Breeding success	Area within radius	Raven (<i>Corvus corax</i>)
Ouin et al. (2004)	Presence	Area within radius	Meadow brown butterfly (<i>Maniola jurtina</i>)
Pope et al. (2000)	Metapop. structure	Area within radius	Leopard frog (<i>Rana pipiens</i>)
Rachlow and Bowyer (1998)	Habitat selection	Euclidean distance ^a	Dall's sheep (<i>Ovis dalli dalli</i>)
Smith et al. (2013)	Presence	Euclidean distance ^a	Koala (<i>Phascolarctos cinereus</i>)
Stewart et al. (2010)	Distribution	Area within radius	Moose (<i>Alces alces</i>)
Zengeya et al. (2014)	Habitat selection	Euclidean distance ^a	Cattle (<i>Bos taurus</i>)

Results from standardized search within Web of Science and Google Scholar using search terms: landscape complementation, resource complementation, habitat complementation, or multiple habitat requirements in March 2017

^a Euclidean distance represents the distance between the focal patch and nearest neighbor of complementary habitat type

characteristics considered in traditional habitat selection models. We further contrasted classic distance metrics with metrics of landscape resistance to determine how the connectivity between habitats influences selection.

A bipartite network approach to landscape complementation

To parameterize a bipartite network for landscape complementation, we first define the nodes of the network as discrete habitat patches defined as two different habitat types, k and m . The links between nodes in a habitat network can be quantified using

observed movements from tracking or observation data (Rhodes et al. 2006; Fortuna et al. 2009), maximum or mean dispersal distance of the focal species (Bunn et al. 2000; Minor and Urban 2008; Lookingbill et al. 2010), or parameters from modeled dispersal kernels (Urban and Keitt 2001; Saura and Pascual-Hortal 2007; Fletcher et al. 2011). Observations of movements between habitat patches, however, can be difficult to obtain (Lookingbill et al. 2010), and the use of maximum distance to quantify links can be misleading and a poor predictor of connectivity (Fall et al. 2007; Fletcher et al. 2011; Moilanen 2011). Therefore, a negative exponential dispersal kernel has often been used in metapopulation theory to describe

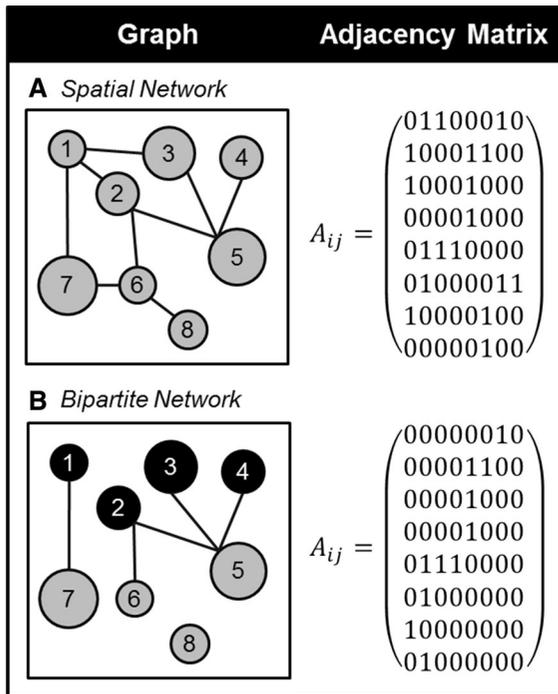


Fig. 1 Example graphs of **a** a classic spatial network, where nodes can link to any other node, and therefore the adjacency matrix (0 no link between nodes, 1 link between nodes) is symmetrical and **b** a bipartite network, where nodes are split into two distinct sets (*black* and *gray*) and links are only between sets, not within sets. The adjacency matrix of the bipartite network contains 0s between nodes of the same set

the probability of a species dispersing to a specific patch based on distance between patches (Hanski 1998). More specifically, this kernel predicts the probability of a link between two habitat patches as:

$$p_{ij}^{km} = \exp(-\alpha d_{ij}^{km}) \tag{1}$$

where p_{ij}^{km} is the probability of a link between patch i of habitat type k and patch j of the other habitat type m ; d_{ij}^{km} represents a distance measure between the two patches; and α scales the distance by the inverse of the average dispersal distance of the focal species. By repeating the calculation for all pair-wise comparisons of patches, we obtain an adjacency matrix representing p_{ij}^{km} for each habitat patch-pair in the network, which can be represented as probabilities or truncated to a binary (0, 1) linkage (Fig. 1). If we replace p_{ij}^{km} with 0 for each pair of like habitat patches within the same habitat type (i.e., when $k = m$), we constrain the links to represent a bipartite network (Fig. 1).

Through the use of network metrics we can quantify the configuration and potential connectivity of habitat patches within a landscape (Gastner and Newman 2006; Rayfield et al. 2011). Metrics deemed appropriate to describe landscape complementation included those that specifically considered the proximity and spatial relationship of patches of the two distinct habitat types, i.e. through the incorporation of distance. Equivalent to patch strength (Rayfield et al. 2011), dispersal flux (F_i^k), a type of metapopulation metric that has been applied to networks (Saura and Pascual-Hortal 2007), describes the sum of probabilities of dispersal between the single habitat patch i^k and all patches of type m within a landscape:

$$F_i^k = \sum_{j=1, i \neq j}^{n^m} p_{ij}^{km} \tag{2}$$

where p_{ij}^{km} is the adjacency matrix that describes the probability of the link between patches i^k and j^m described above in Eq. 1 and n^m is the total number of patches representing the other habitat type (m). We can modify this flux measure using a component of the incidence function model developed in metapopulation ecology (Hanski and Thomas 1994, Hanski 1998) to weigh patches based on area and calculate the area-weighted flux (AWF; Moilanen and Nieminen 2002; Saura and Pascual-Hortal 2007). Weighting by the area of focal patch i^k assumes that patch size influences the attraction to that patch during dispersal (i.e. target effect; Simberloff 1976), while weighting by the area of other patches of the other habitat type (m) within the landscape considers the potential number of migrants available to focal patch i^k (Hanski and Thomas 1994). Area-weighted flux for patch i^k can be described as:

$$AWF_{i^k} = \sum_{j=1, i \neq j}^{n^m} p_{ij}^{km} a_{j^m}^b \left(\frac{a_{i^k}^c}{\bar{a}^k} \right) \tag{3}$$

where a_{j^m} is the area of the other habitat patch j^m , in which patch area relates to propagule pressure (i.e. the larger the patch, the greater possible migrants to patch i^k); a_{i^k} is the area of the focal patch i^k and \bar{a}^k is the mean area of all habitat patches within the focal patch habitat type k that are available to the study species (e.g. within its home range or within traveling distance), representing the influence of the focal patch's area on emigration to that patch (i.e. target

effect); and b and c are constants that scale area parameters in response to their relative influence on movement. While metrics like AWF are potentially helpful for capturing the roles of area and direct linkages, they do not formally capture indirect linkages among patches. To this end, we can also consider eigenvector centrality (λ), which describes the isolation of habitat patches based on the relative importance of the patches they are connected to—i.e. “friends of my friends” (Estrada and Bodin 2008; Newman 2008; Vasudev and Fletcher 2015). Eigenvector centrality can be represented by:

$$x_{i^k} = \frac{1}{\lambda} \sum_{j=1, i \neq j}^{n^m} p_{ij}^{km} x_{j^m} \quad (4)$$

where x_{i^k} is the degree centrality of the focal patch i^k , p_{ij}^{km} is the adjacency matrix of the network, x_{j^m} is the degree centrality of habitat patch j^m , and λ is the leading eigenvector that represents the eigenvector centrality. If we calculate the degree centrality of patch j^m , x_{j^m} , relative to those patches *within* the same habitat type (m), we can represent the topology of all patches within that type; therefore, the eigenvector centrality of patch i^k denotes the connectivity of patch i^k to patches of type m through its connection to patch j^m . When using weighted graphs, however, there comes an issue with using degree centrality as the number of connections; Barrat et al. (2004) therefore recommend using the sum of weights of the connections rather than the number of connections themselves.

Methods

An application to habitat selection by the Florida Manatee

Study area

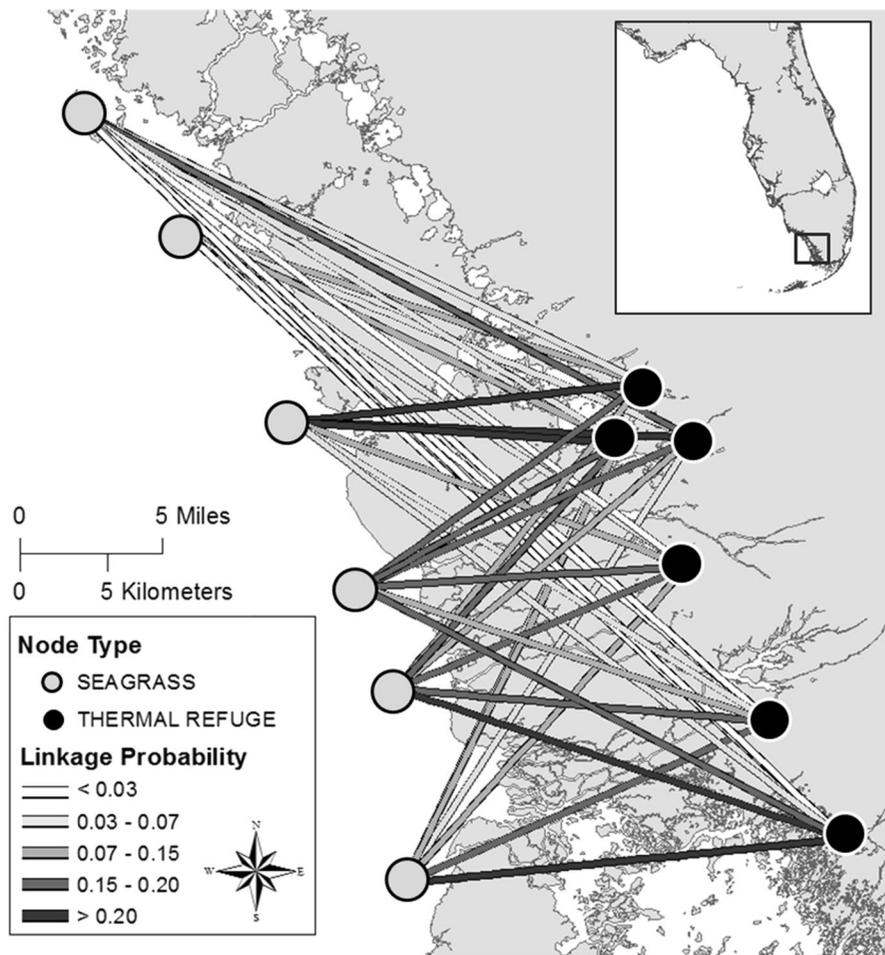
Our application was focused along the southwestern coast of Florida (Fig. 2). The primary shoreline habitat type within this area is mangrove forest assemblages (most common species red mangrove, *Rhizophora mangle*), broken up into shallow inland bays and lakes by inland rivers and canals. Shallow areas offshore provide substrate for seagrass species eaten by manatees, including *Syringodium filiforme*, *Thalassia*

testudium, *Halodule wrightii*, and *Halophila* spp. and macroalgae (Hartman 1979; Slone et al. 2013). Manatees occasionally feed upon freshwater plants and algae within the inner bays and rivers, including *Ruppia maritime*, *Potamogeton* spp, and *Chara* spp.; manatees have also been observed foraging on mangrove leaves and grasses along the river banks (Stith et al. 2012).

Study species

The Florida manatee is an herbivorous marine mammal that feeds primarily on seagrasses and other submerged aquatic vegetation (SAV) within the riverine and estuarine systems along the Florida coast (Packard and Wetterqvist 1986). Due to their diet of SAV, manatees have a low metabolic rate and layer of blubber with low insulative properties, which results in a susceptibility to cold stress in water temperatures as low as 15–20 °C (Irvine 1983). When faced with cold water, manatees seek out warm water in the form of thermal refugia (Campbell and Irvine 1977; Irvine 1983). Most thermal refugia used by manatees in Florida are freshwater springs and the warm-water effluent of power plants (Laist and Reynolds 2005a, b), but in the study area they are primarily passive thermal basins (PTBs) and are found inland within the riverine and estuarine systems of the Everglades and Ten Thousand Islands. PTBs here are relatively small, ephemeral pockets of warm water that remain warmer than surrounding water due to various characteristics; some are deep areas with low current flow that cool slower than surrounding shallower waters, while others are inverted thermal haloclines where a deep layer of warm salty water is trapped by a surface layer of fresh water provided by man-made weirs or freshwater flows (Stith et al. 2011). Access to freshwater vegetation inshore is often limited to areas that are shallow enough for sunlight that penetrates the water column to support photosynthesis and plant growth (Powell and Rathbun 1984). Most freshwater areas in the study region are deep and too dark to support SAV, resulting in foraging locations that rarely coincide with warm water sites needed for thermal refugia (Packard and Wetterqvist 1986). During the winter, manatees have been observed to adopt central-place foraging strategies, resting in thermal refugia for periods of time and periodically travelling out to seagrass beds or other

Fig. 2 The study area of Everglades National Park and the Ten Thousand Island National Wildlife Refuge, with a partial representation of the bipartite network between thermal (gray circles) and forage (black circles) habitats used by the Florida manatee. Colors of the links represent the probability of linkage (p_{ij}^{km}) from the adjacency matrix based on shortest distance and manatee dispersal capabilities (see Eq. 1 and Supplementary Materials)



areas that support SAV growth (Barton 2006; Deutsch et al. 2006). Here we focus only on these movements, assuming that manatees are limited in selection of seagrass and thermal habitats and don't travel between similar habitat types.

Animal location data

Forty free-ranging manatees were captured, radio-tagged, and tracked by the U.S. Geological Survey Sirenia Project (USGS) from 2002–2008 (see Bonde et al. 2012 for capture methodology and Slone et al. 2013 for tracking methodology). The tagging gear consisted of a floating, satellite-linked (www.argos-system.com) GPS tag (www.telonics.com) that was attached with a nylon tether to a padded belt around the peduncle of the animal. Weak links are incorporated in the tether and the belt acting as release points

that would allow the animal to break free if becoming entangled (Reid et al. 1995). Tags remained on individual manatees until they were replaced with newer tags or broke free. GPS locations were recorded every 30–60 min with ~5–10 m accuracy, providing the tag was at the surface of the water; if a manatee dove below the surface during a fix, then the location was not recorded (Slone et al. 2013). We filtered telemetry data to remove fixes before and after the tag was on the animal and any erroneous points associated with excessive speed between fixes (>20 km/h).

Patch-level covariates

We identified habitat patches from shapefiles of previously mapped seagrass beds and newly identified thermal refugia (datum: NAD 1983). Seagrass maps were provided by the Florida Fish and Wildlife

Conservation Commission (FWC; <http://ocean.floridamarine.org/mrgis/>) that were produced from aerial photography and validated by field measurements; we used the most recently updated map from 2010 (resolution: 1:12000 m), which included the greatest area mapped to date (FWRI 2011). Thermal refuge locations were identified from repeated observations of manatee use during the winter and validated by the USGS (JPR and DHS, unpublished; 1:1 m); quality and stability of thermal refugia over the winter was analyzed in a different study (CGH, unpublished).

We calculated area of seagrass patches in ArcGIS 10.3 (ESRI 2011) and thermal refuge depth was field measured during site visits by the USGS. We calculated the distance from each habitat patch to water monitoring stations managed by the USGS National Water Information System, National Park Service, and the South Florida Water Management District and linked tide height (m) and stage (flood, high, ebb, or low) from the closest water station (<10 km) at the date and time of each GPS location within that habitat patch. We used conditions from the closest station to each thermal refuge to represent the water temperature of the surrounding area that a manatee would experience if it was not within the refuge.

Distance between habitat types

We used three different distance measures to describe the distance between habitat patches (d_{ij}^{km}) in our analyses: shortest distance, least-cost distance, and resistance distance (Fig. 3). Both least-cost distance and resistance distance require a raster map of the landscape, in which each cell is a parameterization of the effect of the landscape on movement (McRae 2006). We first reclassified a map of the Florida shoreline using ArcGIS to set a base cost surface layer describing water as no resistance and land as complete resistance. Unlike most terrestrial organisms, manatees are not influenced by many landscape features, with the exception of bathymetry, particularly large seagrass flats, or boat channels (Bauduin et al. 2013). Manatees are restricted to areas with a minimum depth of about 1 m (Edwards et al. 2016); however, the minimum depth of our map was 2 m, and therefore we assumed areas inaccessible to manatees would be noted as land and therefore already considered impassible. Manatees may avoid boat channels to reduce the threat of

collision, but have also been observed to use deep channels while traveling (O'Shea et al. 1985; Nowacek et al. 2004; Martin et al. 2016). We therefore added a layer of boat channels provided by the FWC and buffered the channel by 25 m to represent the area in which manatees have been observed to respond to close boat traffic (Nowacek et al. 2002, 2004). We then modified this layer with varying degrees of resistance values to describe how boat channels may facilitate or impede manatee movement (see Supplementary Materials). Finally, we used the *gdistance* package (van Etten 2012) in R 3.3.1 (R Development Core Team 2016) to calculate the shortest distance (using “shortestPath” and “SpatialLinesLength”; Fig. 3a) and least cost distance (using “costDistance”; Fig. 3b), and Circuitscape toolbox in ArcGIS (McRae and Shah 2009) to calculate the resistance distance (Fig. 3c), between seagrass and thermal refuge habitats through the cost surface layers (Table S1; see Supplementary Materials).

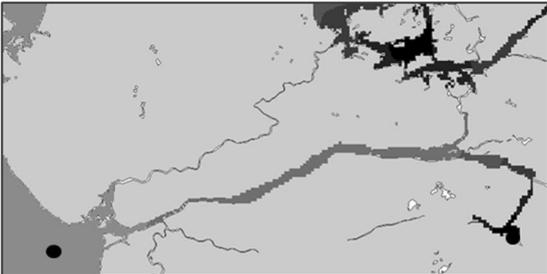
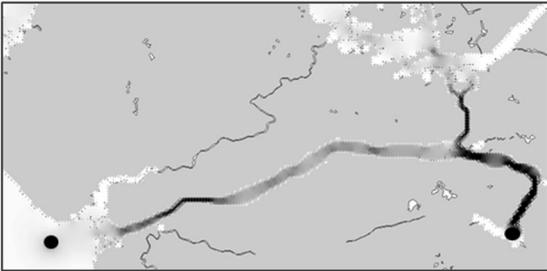
Building a bipartite network

We built a bipartite network using seagrass patches and thermal refugia as nodes and populated the links between them using dispersal kernels taken from metapopulation theory (MacArthur and Wilson 1963; Hanski 1998; Urban and Keitt 2001). Using an independent dataset of GPS locations of manatees from a different area in Florida (Reid et al. 1995), we fit a negative exponential kernel, estimated the inverse scale parameter (α), and then used Eq. 1 to predict the probability of a link between two habitat types (see Supporting Information) and parameterize our adjacency matrix. We used multiple distance values to represent d_{ij}^{km} for each seagrass patch and thermal refuge pair and scaled by α for each distance type. We calculated the three network metrics described above (Eqs. 2–4) for each bipartite pair to include in the models.

Conventional methods used to quantify landscape complementation

To properly compare the quantification of landscape complementation by network metrics to those measures used in previous studies (Table 1), we calculated the nearest-neighbor distance for each focal patch to

Fig. 3 Three distance measures, their description, and the tool and function used to describe connectivity between habitat types of the Florida manatee

Distance Measure	Description
<p>A Shortest Distance</p> 	<p>Shortest geographical distance between two points through a resistance-free landscape, with land as impassible</p>
<p>B Least-Cost Distance</p> 	<p>Shortest path between two points considering the cumulative costs of neighboring cells across a resistance surface</p>
<p>C Resistance Distance</p> 	<p>Shortest path between two points across a resistance surface while incorporating the costs of multiple potential pathways</p>

the nearest patch of its complementary habitat type for each distance measure (shortest, least-cost, and resistance). We also calculated the area of the complementary habitat of that focal patch by summing all complementary habitat areas within a 25 km radius (representing daily manatee movement; Deutsch et al. 2006) around each focal patch.

Modeling habitat selection

To apply these metrics to habitat selection modeling, we used a mixed conditional logistic model as described by Duchesne et al. (2010) to calculate the relative probability of a manatee selecting a patch

among other available patches. Mixed conditional logistic models are a type of discrete-choice model that take the framework of a matched design, which compares the characteristics of an animal's location to that of random locations within a limited area (Duchesne et al. 2010; McCarthy and Fletcher 2015). We modeled habitat selection of both seagrass patches and thermal refugia for manatees during winter months (November–March) for all years (2002–2008), as this is the critical period where manatees require both habitat types (Stith et al. 2011).

We determined habitat use by extracting habitat type at each GPS position by overlaying the seagrass and thermal refuge maps. GPS positions outside of

seagrass or thermal refugia were discarded. Manatees also travel inland to use freshwater resources, which can be difficult to quantify as these resources are not explicitly mapped within southwestern Florida. To avoid misclassifying freshwater use as thermal refuge use, we only used GPS locations within thermal refugia during ambient environmental conditions <20 °C. To circumvent autocorrelation with successive GPS fixes within the same habitat, we collapsed sequential GPS points within the same habitat into a single use measure.

To represent available habitats for each used habitat, we randomly selected five habitat patches of the same habitat type within a Euclidean buffer representing average daily movement of manatees (25 km). For each available habitat, we calculated seagrass area or thermal refuge depth, linked tide height (m) and stage (flood, high, ebb, or low) from the closest weather station (<10 km) at the date and time of the used locations, measured the nearest neighbor distance and the area of the complementary habitat to represent potential bias, and calculated the three bipartite network metrics.

We developed two sets of a priori mixed conditional logistic models using R package *mclogit* (Elff 2017), with one set for each habitat type (seagrass and thermal refugia) to determine the effects of covariates on selection of each habitat type separately. We dropped correlated variables and only included those with correlations $<|0.70|$ in each model (Zar 2010). We compared models including covariates describing focal patch covariates (seagrass area, thermal refuge depth, thermal refuge temperature, and tide stage) with those containing measures traditionally used to describe landscape complementation (nearest neighbor distance between patch and complementary habitat or area of complementary habitat within buffer of focal patch) and those including bipartite metrics (dispersal flux, area-weighted flux, and eigenvector centrality). To determine if the inclusion of landscape resistance better defines proximity to capture the landscape complementation process, we created additional models with least-cost distance or resistance distance in place of nearest neighbor distance. Finally, we contrasted models including conventional landscape complementation measures with the three bipartite network metrics. We centered and scaled covariates to improve convergence of all models. All models contained manatee ID as a random intercept to

control for variation associated with sample size of the tracking data for each manatee. We used Akaike information criterion (AIC) to select among competing models (Burnham and Anderson 2004).

Results

Individual manatees were tracked for an average of 140 days (maximum = 413 days, minimum = 4 days); two animals were tracked <14 days and were removed from all analyses, reducing our sample size from 40 to 38 individuals. The number of successful GPS fixes per animal averaged 5,816 (minimum = 388 fixes, maximum 22,923 fixes), with a total of 106,305 fixes used in the analyses. Forty-two seagrass patches and 14 thermal refugia were identified as being used by manatees during the tracking period, i.e. 2000–2008. The mean distance between selected forage and thermal habitats was 16.34 km, with area of selected seagrass patches averaging 43.18 km² (7.98–90.26 km²) and thermal sites 1.73e–5 km² (2e–6 to 3.3e–5 km²).

The models containing covariates for area metrics (focal patch area), proximity metrics (resistance distance), and network metrics (eigenvector centrality) had better fits than models containing conventional complementation measures (nearest-neighbor distance or area of complementary habitat) or focal patch area alone (Table 2). Of the models describing selection of seagrass habitats, those that contained patch area as a covariate had the lowest AIC values of models containing distance measures or network metrics alone. Additionally, those models containing network metrics related to habitat area (area-weighted flux) had low AIC values compared to other network metrics (Table 2). However, the top three models for seagrass selection all contained eigenvector centrality as a covariate, indicating the importance of the inclusion of network metrics. The top models describing selection of thermal habitats contained covariates of resistance distance, with AIC values lower than those models containing shortest or least-cost distance (Table 2). Furthermore, there was little support for either negative or positive effect of boat channels on manatee movement, as resistance distances using water and boat channels at equal cost values (Table S1) described selection probabilities better than shortest distance or least-cost distance and

resistance distances that considered the facilitation or hindrance of boat channels (Table 2, Table S2). Finally, those models for thermal refugia selection that included network metrics such as dispersal flux or eigenvector centrality resulted in lower AIC values than resistance distance alone, which coincides with seagrass models in the importance of network metrics on selection. The inclusion of both proximity and network metrics in the top models suggests that neither

network metrics nor distance measures alone properly quantify landscape complementation.

We estimated a positive effect of both patch area and eigenvector centrality on selection of both seagrass and thermal refugia (Fig. 4, top and middle), indicating that manatees increased their use of seagrass and thermal habitats that were larger and highly connected to the other habitat type. Effects of resistance distance differed between selection of

Table 2 Habitat selection models for seagrass and thermal habitats for the Florida manatee and respective Δ Akaike information criterion (Δ AIC), log-likelihood values (LL), and number of parameters (k)

Model covariate	Seagrass			Thermal refuge		
	Δ AIC	LL	k	Δ AIC	LL	k
Area metrics						
Patch area	193.3	-930.9	2	317.3	-458.5	2
Complementary patch area	2152.8	-1910.6	2	305.2	-452.5	2
Proximity metrics						
Shortest distance	2161.8	-1915.2	2	316.7	-458.3	2
Least-cost distance	2180.0	-1924.2	2	283.9	-441.8	2
Resistance distance	1949.7	-1809.1	2	8.0	-303.9	2
Network metrics						
Dispersal flux (shortest distance)	1039.2	-1353.9	2	317.3	-458.6	2
Dispersal flux (least-cost distance)	1626.0	-1674.1	2	303.9	-454.4	2
Dispersal flux (resistance distance)	2178.6	-1923.6	2	275.5	-436.6	2
Area-weighted flux (shortest distance)	1317.0	-1492.7	2	302.9	-451.3	2
Area-weighted flux (least-cost distance)	460.6	-1091.4	2	310.9	-455.3	2
Area-weighted flux (resistance distance)	577.4	-1123.0	2	282.6	-444.2	2
Eigenvector centrality	1803.8	-1735.2	2	317.0	-458.4	2
Combination of metrics						
Patch area + eigenvector centrality	169.6	-918.1	3	318.0	-457.9	3
Patch area + least-cost distance + eigenvector centrality	15.4	-866.7	4	286.2	-438.5	4
Patch area + resistance distance + eigenvector centrality ^a	0.0	-832.3	4	0.0	-297.2	4
Shortest distance + dispersal flux	852.2	-1259.4	3	320.0	-458.0	3
Resistance distance + dispersal flux	1021.2	-1343.9	3	8.3	-302.5	3
Shortest distance + area-weighted flux	1140.4	-1403.5	3	306.0	-451.2	3
Least-cost distance + eigenvector centrality	1711.2	-1715.7	3	279.3	-438.6	3
Resistance distance + eigenvector centrality	1398.4	-1532.5	3	2.1	-298.9	3
Complementary patch area + dispersal flux	824.3	-1245.4	3	306.9	-452.3	3
Complementary patch area + area-weighted flux	1169.0	-1417.8	3	298.6	-448.2	3
Complementary patch area + eigenvector centrality	1730.9	-1698.7	3	307.1	-452.5	3

All models had a random effect of manatee ID

^a Denotes top model for both seagrass and thermal habitats

seagrass or thermal habitats; we estimated significant negative effects of resistance distance for seagrass as expected, but significant positive effects for thermal refugia (Fig. 4, bottom).

Discussion

The influence of landscape complementation on animal populations has been recognized in ecology for decades (Dunning et al. 1992). Yet most research assumes that animal processes relevant to landscape complementation are driven by proximity or area

effects alone and often fail to capture the underlying effects of the spatial configuration of different habitats relative to each other (see Table 1). Currently, ecological models do not harness developments in network analysis to better interpret the role of landscape complementation. Spatial networks offer a framework to address the complexity of landscape complementation while considering the spatial relationship of habitats (Fig. 2). Here we used a bipartite network framework to ask if the inclusion of spatial configuration and connectivity of habitats better describes habitat selection behaviors compared to focal patch covariates alone. We found that the inclusion of both resistance distance and eigenvector centrality best predicted patch selection by describing the proximity and connectivity of that patch to the other habitat type.

Application to habitat selection models for the Florida manatee

Metrics describing the characteristics of a single habitat do not capture the importance of landscape complementation when species require two distinct habitats to fulfill different needs (Dunning et al. 1992). This requirement often has high bioenergetic consequences when an animal may be faced with a trade-off between selecting high-quality forage patches and closer, lower quality foraging patches (Choquenot and Dexter 1996). Manatees have been observed to decrease foraging efforts with increased distances between seagrass patches and thermal refugia when exposed to cold water temperatures (Edwards et al. 2016, Haase 2016). By selecting closer habitats, manatees are able to use both habitats and minimize travel time. This type of pattern has also been observed in wild pigs (*Sus scrofa*), where reproductive rates were not explained entirely by forage patch quality, but rather by the combination of quality and distance to riverine woodlands (Choquenot and Ruscoe 2003). Wild pigs utilize riverine woodlands as thermal refugia to offset high heat loads, and like manatees, select foraging areas that are more interspersed with these critical habitats. Areas that provide both foraging opportunities and thermal refugia within close proximity allowed for exploitation of both habitats and thus supported larger populations.

Our results suggest that not only do manatees know where their resources are located, but they may understand the spatial relationship of each habitat to

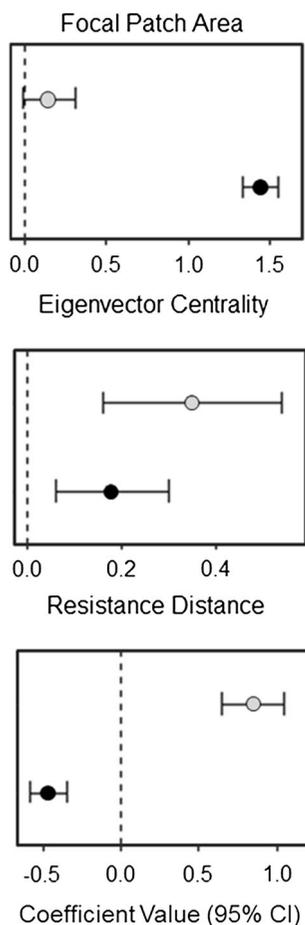


Fig. 4 Coefficient values and 95% confidence intervals for patch area, eigenvector centrality, and resistance distance covariates of the best model predicting selection of thermal refugia (gray circles) and seagrass habitat (black circles). Positive and negative coefficient values (above or below the dashed line representing 0) indicate an increase or decrease in the relative probability of use in response to an increase of that covariate

the other type. For instance, eigenvector centrality was a significant predictor of habitat selection of thermal refugia, which indicates that manatees select refugia that are connected to multiple seagrass beds through indirect links. Understanding not only where their habitats are, but how they are spatially distributed throughout the area is critical for efficiently using each habitat during stressful periods. This knowledge of the location of habitat types is thought to be gathered by young manatees during their first winter season dependency as calves follow their mothers between foraging grounds and thermal sites (O'Shea and Kochman 1990). Repeated observations of manatees revisiting the same thermal sites within a single winter season and returning to these sites year after year support our assumption that manatees maintain a cognitive map of their resources (Reid et al. 1991; Deutsch et al. 2003). The familiarity of the spatial configuration of forage and thermal sites and connectivity between them is critical for manatees to survive through the winter—selection of foraging habitats or thermal refugia that are farther away or not highly connected can result in greater energetic demands to travel between them. Further research determining the energetic effects of exploratory movements versus direct movements between habitat types in the winter is warranted.

More information about habitat quality would provide a better means to explicitly test how animals respond to trade-offs associated with the requirement of two habitats. Analyses into the specific forage species selected by an individual and correlations with forage nutritional quality could result in more robust model predictions by explicitly linking the quality of the habitat to selection events. Likewise, the positive influence of resistance distance on selection of thermal habitat is assumed to be an artifact of increased thermal refuge quality farther inland. Analyses are limited to known habitats and habitat visited by the individuals in this study; further developments describing the entirety of a study system in regards to habitat mapping and delineation of habitat quality would also strengthen our predictions.

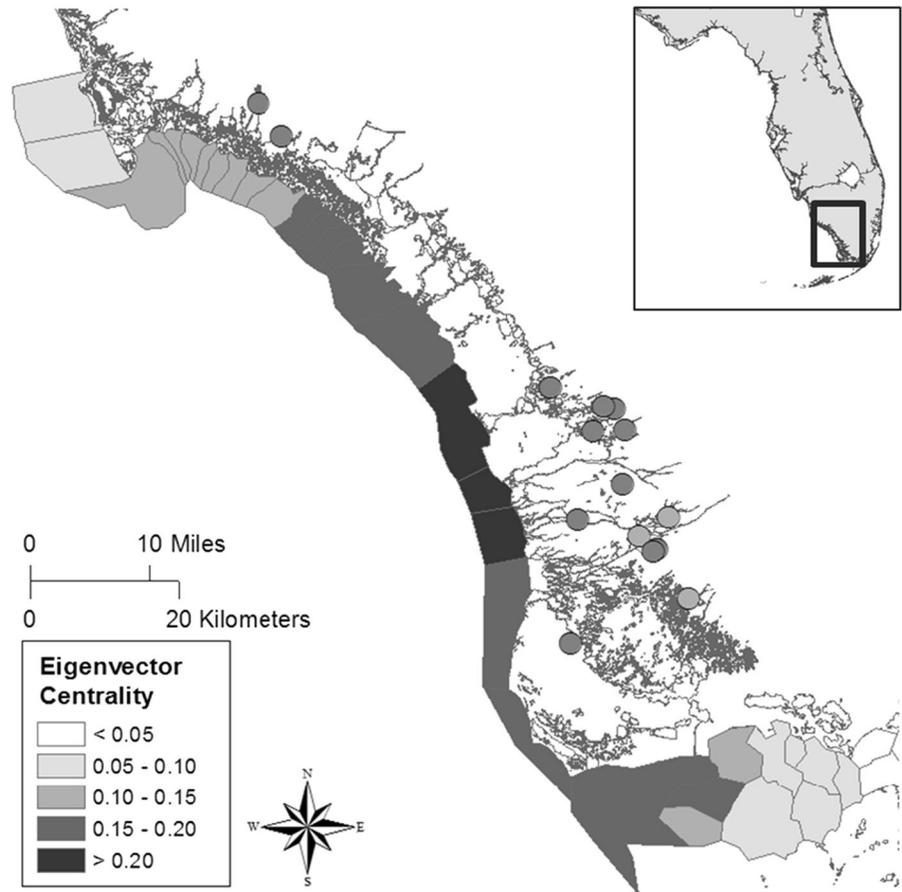
The bipartite approach to landscape complementation

Our approach expands on previous metrics of landscape complementation by incorporating the

connectivity of the habitat network. Previous applications of landscape complementation that focused on the shortest distance to the nearest complementary patch fail to account for connectivity issues associated with landscape features that impede movement between patches. Our results show that resistance distance is more appropriate for describing selection as it considers the likelihood the animal can move about the landscape. This is not surprising, as the inclusion of multiple pathways in describing connectivity between habitat patches has been shown to better predict animal movement (Fletcher et al. 2014) and gene flow (McRae and Beier 2007), compared to shortest distance alone. Multiple pathways increase the opportunities for animals to travel between habitats, especially in areas such as the Everglades where narrow waterways may become impassible due to tides.

Eigenvector centrality, or the importance of a patch based on the importance of the patches it is connected to, describes the connectivity of one habitat type to its complementary habitat by means of its indirect links. Describing the configuration of these habitats using eigenvector centrality quantifies the topology of habitats in relation to a single selected patch, and weights the importance of clustering in its calculation. In this system, it is unsurprising that manatees select thermal refugia with high eigenvector centrality, as they are connected to seagrass patches that are highly connected with other seagrass patches. Eigenvector centrality goes beyond describing proximity or area-effects typically described with conventional measures of landscape complementation by taking into account the topology of a single habitat and its connection to its complementary habitat while considering the dispersal capabilities of the animal in question. Other measures, such as the presence or the proportion of one habitat within a set radius of the other, are more likely to describe the composition of habitat types, rather than the configuration (Choquenot and Ruscoe 2003). Bipartite network metrics, such as eigenvector centrality, capture the spatial topology of the habitat network and better describe the spatial relationship of these two distinct habitat types (Urban and Keitt 2001; Estrada and Bodin 2008). Evaluating habitat selection of a focal patch while only considering the effects of the characteristics of that focal patch fails to properly address the dependence on multiple habitats and can be misleading in the model's

Fig. 5 The complementation index (i.e. eigenvector centrality) of seagrass patches (*polygons*) and thermal refugia (*circles*) throughout the study area



assessment of important predictors of habitat use (Pope et al. 2000; Choquenot and Ruscoe 2003; Mueller et al. 2009).

The lack of recognition of the spatial configuration of habitats and the connectivity between them in habitat selection may be due to patch-focused management practices and assessment at inappropriate scales (Estrada and Bodin 2008; Mueller et al. 2009). In instances where close proximity of two habitats is important to habitat selection, understanding the configuration of these habitats is critical in properly assessing habitat use (Haynes et al. 2007). Furthermore, eigenvector centrality, in addition to the connectivity of habitats, can be used as a means to map habitats for conservation purposes (Fig. 5), with precedence on those habitats with greater “complementation indices” that support larger populations (Dunning et al. 1992).

Here, we provided a framework to quantify landscape complementation and incorporate a spatially explicit component of habitat configuration to describe selection of two required habitats. We have shown that complementation is an important predictor of selection and that classic complementation measures are not sufficient in describing the process (Taylor et al. 1993). Rather, quantifying the connectivity between habitat types via a bipartite network provides a means to assess the impacts of this reliance on two required, yet spatially-separated habitats.

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