APPLICATION





Operationalizing ecological connectivity in spatial conservation planning with Marxan Connect

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Abstract

- 1. Globally, protected areas are being established to protect biodiversity and to promote ecosystem resilience. The typical spatial conservation planning process leading to the creation of these protected areas focuses on representation and replication of ecological features, often using decision support tools such as Marxan. Yet, despite the important role ecological connectivity has in metapopulation persistence and resilience, Marxan currently requires manual input or specialized scripts to explicitly consider connectivity.
- 2. 'Marxan Connect' is a new open source, open access Graphical User Interface (GUI) tool designed to assist conservation planners with the appropriate use of data on ecological connectivity in protected area network planning.
- 3. Marxan Connect can facilitate the use of estimates of demographic connectivity (e.g. derived from animal tracking data, dispersal models, or genetic tools) or structural landscape connectivity (e.g. isolation by resistance). This is accomplished by calculating metapopulation-relevant connectivity metrics (e.g. eigenvector centrality) and treating those as conservation features or by including the connectivity data as a spatial dependency amongst sites in the prioritization process.
- 4. Marxan Connect allows a wide group of users to incorporate directional ecological connectivity into conservation planning with Marxan. The solutions provided by Marxan Connect, combined with ecologically relevant post-hoc testing, are more likely to support persistent and resilient metapopulations (e.g. fish stocks) and provide better protection for biodiversity.

KEYWORDS

decision support software, demographic, ecological connectivity, Marxan, migration, movement ecology, spatial conservation planning, structural connectivity

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1 | INTRODUCTION

Connectivity, in its most general form, refers to the exchange of individuals (including genes, traits, disease, etc.), energy or materials among habitat patches, populations, communities or ecosystems. Including connectivity in conservation planning can improve population resilience to disturbance, increase metapopulation viability, promote genetic diversity and maintain energetic pathways among ecosystems (Figueira & Crowder, 2006; Lowe & Allendorf, 2010; Palumbi, 2003).

There are many metrics and methods to evaluate the connectivity of sea- and landscapes and these can be used to assess and develop networks of protected areas (Beger, Grantham, et al., 2010; Chollett et al., 2017; D'Aloia et al., 2017; Saura & Pascual-Hortal, 2007; Zeller et al., 2018). The quantity and quality of empirical data used to calculate connectivity metrics have grown rapidly (Hussey et al., 2015; Kool, Moilanen, & Treml, 2013; Magris et al., 2018; Zeller et al., 2018). However, connectivity is not commonly being incorporated in on-theground decision making for conservation or protected area planning (Balbar & Metaxas, 2019; Barnes, Glew, Wyborn, & Craigie, 2018; Beger, Grantham, et al., 2010).

Spatial conservation prioritization is an approach that guides the efficient allocation of conservation resources to areas identified as important for biodiversity (Margules & Pressey, 2000; Moilanen, Wilson, & Possingham, 2009; Wilson, Cabeza, & Klein, 2009). Spatial prioritization often relies on the use of decision-support software (e.g. Marxan or Zonation) to help decide the location of actions (e.g. establishing protected areas), often while minimizing the conservation impact on resource users. These tools are primarily used to develop representative and cost-efficient conservation plans that meet predefined targets for species and/or habitats (but also cultural sites, processes, and socio-economic features).

Traditionally, the consideration of connectivity in spatial planning has focused on patterns, primarily expressed by spatial adjacency. More recently, approaches to include processes associated with ecological connectivity in spatial decision support software have emerged (Beger, Linke, et al., 2010; Chollett et al., 2017; Moilanen, Leathwick, & Elith, 2008; White, Botsford, Hastings, & Largier, 2010) and new tools developed for specific systems and species (e.g. Beger, Linke, et al., 2010; Chollett et al., 2017; Krueck et al., 2017; Moilanen et al., 2008; White et al., 2010) whose outputs can be integrated into existing planning workflows. However, their incorporation into common decision-support frameworks and tools remains technically challenging and typically requires customized coding and work-arounds which can hinder their inclusion in spatial planning processes. To build broad capacity in the conservation community for including ecological connectivity into spatial planning processes, technical documentation, best-practice guidelines and user-friendly tools are urgently needed.

Our objective is to develop a conceptual overview of the selection and treatment of connectivity data and to close the capacity gap for its use in spatial conservation prioritization in relation to Marxan, one of the most-widely used spatial planning tools delivering outcomes for conservation planning worldwide (Sinclair et al. 2018). Here, we first discuss the types and treatments of connectivity that can be included

in spatial prioritization and then introduce a new open source tool (under MIT License [https://github.com/remi-daigle/MarxanConnect/blob/master/LICENSE]), called Marxan Connect, to help users operationalize these concepts and data. This manuscript refers to Marxan Connect v1.0.0 of the software.

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2 | UNDERSTANDING CONNECTIVITY DATA

Before we can discuss the capacity of Marxan Connect, some consideration of connectivity data is required. One of the challenges associated with integrating data of ecological connectivity in spatial planning is the wide variety of entities that move (e.g. organisms, genes, pollutants) and of movement processes (e.g. animal migration, larval dispersal, multi-generational gene flow, carbon flux). While there are many types and sources of data, connectivity data are most often expressed as matrices, where donor (or source) sites are rows, and the recipient (or destination) sites are columns. Alternatively, connectivity data may be stored in an edge list where the first column contains the donor site's unique identifier (IDs), the second column contains the recipient site's IDs, and the third column contains the connectivity value (additional columns may contain additional edge attributes). Most common data sources can be analysed in Marxan Connect (e.g. connectivity matrices from dispersal modelling studies or edge lists from animal tracking data). Details on data format (https://marxanconnect. ca/glossary.htmldata formats), types (https://marxanconnect.ca/ glossary.htmldata_formats), mathematical representations and associated assumptions can be found on the Marxan Connect website, marxanconnect.ca (https://marxanconnect.ca/glossary.html data formats).

Some spatial planners may have access to detailed connectivity information based on demographic data. Whether the movement is being measured directly (e.g. individual tagging and tracking) or estimated (e.g. graphic connectivity' (see marxanconnect.ca, https://marxanconnect. ca/glossary.htmldata_types for more details on the mathematical representations of connectivity data). The strength of connectivity is measured as either a probability or absolute amount. Marxan Connect can also generate estimates of the strength of 'landscape connectivity' (e.g. spatial isolation) based either on the Euclidean distance between habitats, or isolation by resistance (McRae, 2006). The probability of connectivity then becomes 1/distance², if pairs of planning units contain the same habitat type, and are normalized for each source planning unit so that the sum of probabilities equals 1 (i.e. row normalized). This is important, because Marxan Connect always assumes larger values to represent stronger connectivity regardless of input.

3 | USING CONNECTIVITY DATA IN SPATIAL PRIORITIZATION

Marxan (Ball, Possingham, & Watts, 2009) analyses discretized landor seascapes into 'planning units' and solves an objective function Methods in Ecology and Evolution DAIGLE ET AL.

to find sets of sites that meet representation targets for features while minimizing impacts to people (also called 'costs'; see Box 1 for more details). In addition to the often used 'rules of thumb' for connectivity which guide sizing and spacing of protected areas in datalimited cases (Mora et al., 2006; Smith & Metaxas, 2018), there are several different quantitative methods to directly incorporate connectivity data into the standard Marxan workflow (Figure 1).

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These include: (a) treating connectivity properties of planning units as conservation features for which a target is set; (b) including connectivity strengths among planning units as spatial dependencies within the objective function; (c) treating connectivity properties of planning units as a connectivity cost; and (d) customizing the objective function to incorporate connectivity performance metrics. In Marxan Connect, methods (a) and (b) are fully implemented and

BOX 1 A primer for spatial conservation planning

Marxan (Ball et al., 2009) uses a simulated annealing algorithm to find good solutions to the "minimum set" problem. In the minimum set problem, the user specifies an amount of each conservation feature j that needs to be conserved, or conservation targets (T_j), for each conservation feature. The basic minimum set problem can be solved with integer linear programming and does not consider connectivity:

minimize
$$\sum_{i=1}^{N} c_i x_i$$
, given that we should meet all targets

$$\sum_{i=1}^{N} x_i r_{ij} \ge T_j, \text{ for all features } j,$$

where N is the number of planning units, c_i is the cost of planning unit i, r_{ij} is the amount of feature j in planning unit i, and x_i is a control variable which has the value of 1 for selected sites and 0 for unselected sites. It is usually desirable to include some basic spatial properties of a protected area system such as geographic proximity or adjacency information between planning units to help minimize costs or maximize clumping of a protected area system. For example, if the common boundary between every pair of planning units is known, then the minimum set problems can be extended to include a term for the boundary length of the reserve system and an effort made to minimise it:

minimize
$$\sum_{i=1}^{N} c_i x_i + b \sum_{i=1}^{N} \sum_{h=1}^{N} x_i (1-x_h) cv_{ih}$$
, given that we should meet all targets

$$\sum_{i=1}^{N} x_i r_{ij} \ge T_j, \text{ for all features } j,$$

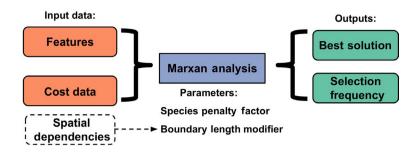
where b is the boundary length modifier (BLM), and cv_{ih} represents the cost of a boundary and is typically the length of the physical boundary between sites i and h. Costs (c_i) in Marxan often pertain to socio-economic implications of protecting a site, such as management or opportunity costs. For more information see Ball et al. (2009) and Ardron, Possingham, and Klein (2010). Key terms and definitions:

- Planning area: the spatial domain over which the planning process occurs. This is synonymous with terms "domain" or "extent" or "study area" in other fields. This area is subdivided into smaller "Planning Units".
- *Planning unit*: spatial units within the entire planning area (i.e. domain, or study area), which can be defined using regular gridded (e.g. hexagonal) or using landscape features-based (e.g. reefs, water catchments) as in Marxan.
- Boundary Length: the shared boundary length between adjacent planning units.
- Boundary Length Modifier (BLM): a weighting parameter to 'tune' the influence of the boundaries. The BLM helps achieve "clumped" solutions by reducing the overall edge to area ratio. A higher BLM value results in a more 'clumped' Marxan solution.
- Conservation feature: the features (e.g. habitats, species, processes) for which a target is set.
- Conservation target: the minimum quantity or proportion of the conservation feature in the study area to be included in solutions.
- Cost: the cost of including a planning unit in the reserve design. Can be defined as simply as the planning unit area, as the actual fiscal cost required to purchase the land, or as the opportunity cost of displaced incompatible ecosystem uses.
- Solution: a binary output of Marxan reflecting whether a planning unit is selected (1) or not selected (0) as part of the conservation plan.
- Selection frequency: the summed solution output of Marxan reflecting how many times a planning unit was selected across runs.

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Standard Marxan workflow



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Marxan Connect workflow

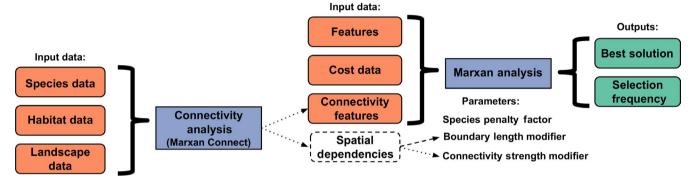


FIGURE 1 Comparison of workflows between the "representation only" standard approach to Marxan and "Marxan Connect." Marxan Connect facilitates the use of connectivity data, derived from animal tagging data, genetics, dispersal models, resistance models, or geographic distance, by producing connectivity metrics and connectivity strengths (i.e. connectivity-based spatial dependencies that are used in the place of boundary definitions) before running Marxan. These connectivity metrics and linkage strengths (independently or in conjunction) are then used as inputs (connectivity-based conservation features or spatial dependencies) in a conventional Marxan workflow. The cost data in the traditional Marxan analysis refer to the cost of protecting a planning unit (i.e. opportunity cost), not the cost to traverse a landscape

facilitated (see below), while Marxan Connect does not facilitate method (c) for reasons described below. Method (d) is currently an area of active research and is yet to be implemented.

A simple and accessible way to integrate connectivity data into spatial planning is to treat it as a conservation feature, such that r_{ii} is the amount of connectivity feature *j* (e.g. reproductive output) in planning unit i. In the classical minimum set problem implemented in Marxan, a representation target is set for each feature, T_i, (e.g. 50%) as a threshold to be met by the reserve design (Ball et al., 2009; D'Aloia et al., 2017). Another approach to incorporate connectivity in Marxan is using directional connectivity data to inform the boundary cost (cv_{ib}). This cost signifies the penalty associated with protecting one site, i, but not protecting other sites to which it is strongly connected, h (Beger, Linke, et al., 2010). Marxan Connect relies on Marxan (v 2.4.3) and can only accept one type of spatial dependency. This means users must choose between either accounting for ecological connectivity or spatial congruence when defining spatial dependencies. A third option is to use the inverse of connectivity values as the cost to be minimized (Krueck et al., 2017; Weeks, 2017), or combined into an integrative performance metric (e.g. T in Krueck et al., 2017) followed by calibration. However, this approach ignores spatial dependencies between the protected sites while simultaneously precluding the incorporation of other cost data directly (e.g. socio-economic or cultural costs).

4 | MARXAN CONNECT

Marxan Connect is designed to help conservation practitioners incorporate connectivity into Marxan analyses (Figure 1). Marxan Connect has a graphical user interface (GUI) that organizes the workflow of this process into six steps (tabs within the GUI): (a) Spatial Input, (b) Connectivity Input, (c) Connectivity Metrics, (d) Pre-Evaluation, (e) Marxan Analysis, and (f) Plotting Options. In addition, Marxan Connect can export data products (e.g. connectivity metrics, Marxan files, etc) at any step to allow users the flexibility to conduct (all or part of) their workflow inside or outside of the Marxan Connect GUI. Below we define these six steps in more detail:

1. Spatial Input allows users to identify and load their planning units, and optionally, define spatially explicit areas to avoid or focus on. An 'avoidance area', for example, may be an area heavily impacted by undesirable activities or threats (e.g. international shipping ports with high risk of invasion by a non-native species), or areas that are potential sources of pollutants (e.g. oil extraction, river outflows). In these 'avoidance' cases, one might wish to prioritize planning units that receive fewer individuals from these avoidance areas. Conversely, a 'focus area' may represent an existing protected area, critical habitat for

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threatened species, and/or otherwise important habitats for connectivity (e.g. nursery grounds, genetically unique and potentially adaptively advantageous populations) that holds value for inclusion in the final spatial plan. Both the avoidance and focus areas can be 'locked in', or 'locked out', but the default is 'status-quo' where Marxan Connect keeps the status of the original planning unit (i.e. defined in pu.dat).

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- 2. Connectivity Input allows users to enter their own demographic (e.g. number of individuals moving from site A to B; see glossary for data types [http://marxanconnect.ca/glossary.htmldata_types]) or landscape-based (e.g. isolation by resistance) connectivity data, generate landscape-based data, or rescale demographic-based data. However, rescaling connectivity data demands working knowledge of the underlying assumptions, and can be problematic (i.e. does the rescaled data accurately represent the connectivity process and spatial context of interest?). To avoid making inappropriate assumptions (e.g. resolution, neighborhood size, extrapolation), it is preferable and more appropriate to collect or generate the connectivity data at the resolution of the planning units. For landscape connectivity, Marxan
- Connect calculates connectivity metrics from networks, based either on Euclidean distance or least-cost paths between the centroids of planning units. However, other software packages such as Circuitscape (McRae, Shah, & Mohapatra, 2009) and Conefor (Saura & Torné, 2009) currently provide a richer set of options and specialized methods. These software packages can be used to create custom conservation features or connectivity matrices both of which can then be used in Marxan Connect. For example, one could create a network using current density (i.e. estimate of connectivity strength using electrical circuit theory) between planning unit centroids based on landscape resistance (i.e. habitat specific resistance to movement) with Circuitscape and input the resulting connectivity matrix into Marxan Connect to create conservation features or spatial dependencies (e.g. flows between planning units).
- 3. Connectivity Metrics guides users in selecting their choice of metrics to include connectivity in their spatial prioritizations (e.g. centrality), calculates the specified connectivity metrics, and establishes how these data are to be treated in Marxan (e.g. as a conservation feature or spatial dependencies; Figure 2).

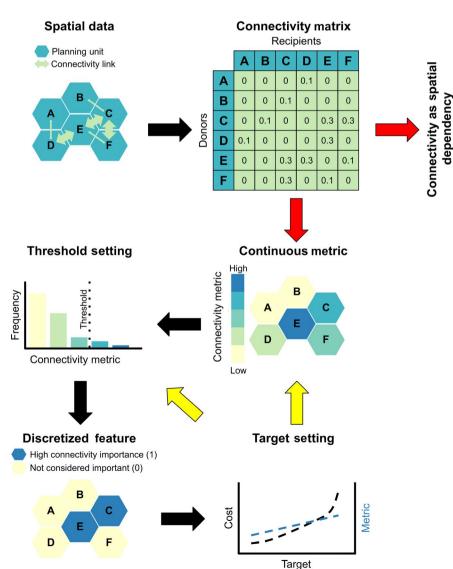


FIGURE 2 Data processing workflow for two possible methods for using raw connectivity data in spatial prioritization: (1) Connectivity as Spatial Dependency in the objective function (Spatial Data → Connectivity Matrix → Connectivity as Spatial Dependency), or (1) Discrete conservation features (Raw Data → Connectivity Matrix → Continuous Metrics → Threshold Setting → Discrete Feature → Target Setting). Black Arrows indicate a logical workflow, while red and yellow indicate a decision point. Red arrows indicate the conservation feature versus connectivity strength method decision point and yellow arrows new metric or new threshold decision point after target setting and post-hoc evaluation of conservation success

Definitions of the metrics to be used as conservation features (e.g. self-recruitment, eigenvector centrality) can be found in the Glossary (http://marxanconnect.ca/glossary.htmldata_formats) or by using the dropdown menu in the tab for this step. After calculating the new metric, users can skip ahead to the Plotting Options for visualization.

- 4. Pre-Evaluation allows users to discretize (i.e. recoding continuous data to categorical), edit, and remove connectivity metrics calculated in the previous step. To create a discrete feature, minimum and maximum threshold values must be chosen specific to the continuous connectivity metric, ideally after an ecological assessment or sensitivity analysis (Ardron et al., 2010). The planning units that meet the threshold(s) are then drawn into unique features for which a target is set (Figure 2). Similarly, this type of threshold setting is often used with species distribution models (Liu, Newell, & White, 2016), where each planning unit is assigned a probability of species occurrence, and a threshold value is used to convert these continuous probability data to a binary map (presence vs. absence or suitable vs. unsuitable) to represent a particular species as a conservation feature (e.g. Minor et al., 2008).
- 5. Marxan files allows users to export new Marxan files (i.e. puvspr. dat, spec.dat, bound.dat, and pu.dat) or append the new data to an existing set of Marxan files.
- 6. Marxan Analysis allows users to generate a Marxan input file (i.e. input.dat) before calling and executing Marxan (Ball et al., 2009) from Marxan Connect. See Box 1 for a primer on Marxan.
- 7. Plotting Options allows users to plot connectivity metrics and Marxan outputs, and export maps and shapefiles that contain the above metrics and results. We recommend visualizing inputs and outputs frequently, particularly after calculating discretized metrics.

As an alternative to the Marxan Connect GUI, we also provide a command line based python module, marxanconpy (https://remidaigle.github.io/marxanconpy/) (v1.0.0), which contains all of the functions of the GUI. Users can use this to create customized reproducible and flexible workflows. The GUI and the python module can also be used in conjunction; for example, the GUI could be used for exploratory analyses and the resulting Marxan Connect project file (.MarCon) can be read into python as a JSON (JavaScript Object Notation) file to serve as the basis for a command line based python workflow.

We purposefully do not provide guidance with respect to the selection of data sources (e.g. models, tagging), available methods (conservation features vs. spatial dependencies), or metrics (e.g. betweenness centrality) because the selection will be dependent on the local ecosystem and data constraints. For example, the spatial dependencies method has the potential to exclude isolated sites from the final solution, depending on the connectivity strength modifier, unless these sites are included using other methods (e.g. a conservation feature for an isolated site that happens to also contain a unique species; Beger, Linke, et al., 2010). This exclusion is a consequence, analogous to the outcome of a large increase the Boundary

Length Modifier. In Marxan Connect, one can combine the use of connectivity as spatial dependencies with a locked-in 'Focus Area' (e.g. an existing protected area, or isolated sites) to accomplish additional design objectives such as maximizing possible stepping stones to other sites, or including species-specific needs. Conversely, the conservation features method may provide more effective reserve design with respect to population dynamics (White, Schroeger, Drake, & Edwards, 2014). Since the literature comparing the efficacy of these approaches is sparse, we recommend users construct and compare multiple conservation scenarios that use local connectivity data in different ways before settling on an approach.

GREAT BARRIER REEF CASE STUDY

To demonstrate the Marxan Connect workflow with minimal data requirements, we present an original Marxan analysis from the Great Barrier Reef (Figure 3). Bioregions for the area (Fernandes et al., 2005) are used as representation-based conservation features to which we add a connectivity-based conservation feature (eigenvector centrality) based on landscape connectivity (i.e. isolation by resistance). A detailed illustration is available in the "Conservation Features + landscape data" tutorial (https://marxanconnect.ca/ CF_landscape.html), as well as other examples on marxanconnect.ca (https://marxanconnect.ca/).

The representation-based workflow uses individual reefs as planning units (Figure S1) and conservation targets of 20% were set for 20 bioregions as in Beger, Linke, et al. (2010). We generated connectivity data using an isolation by distance function in Marxan Connect to estimate the proportion of individuals originating from a donor planning unit that arrive into a recipient planning unit (i.e. probability matrix). This function generates one probability matrix per habitat type; in this case, habitat types correspond to the bioregions used as conservation features. For this example, the values of habitat (bioregion) specific landscape connectivity were averaged to simplify plotting. For some conservation applications, it may be more appropriate to add connectivity-based conservation features for each habitat type as this avoids generalization of averaging connectivity values across features.

In this example, we calculated betweenness centrality from the average probability matrix and used it as the only connectivity-based conservation feature (Figure 3). As with the connectivity-based spatial dependencies method, this approach would lead to low selection frequency for isolated sites unless they are selected to achieve targets for other conservation goals. However, it should be noted that multiple connectivity-based conservation features can be used simultaneously, each representing different aspects of ecological connectivity (i.e. local retention vs. betweenness centrality vs. source strength) or multiple species (highly mobile vs. sedentary species). Additionally, multiple methods for including connectivity could be used simultaneously, but some combinations may be redundant or inappropriate (e.g. eigenvector centrality as a conservation feature and connectivity-based spatial dependencies), thus, we encourage careful consideration of objectives and data prior to implementing the Marxan Connect workflow.

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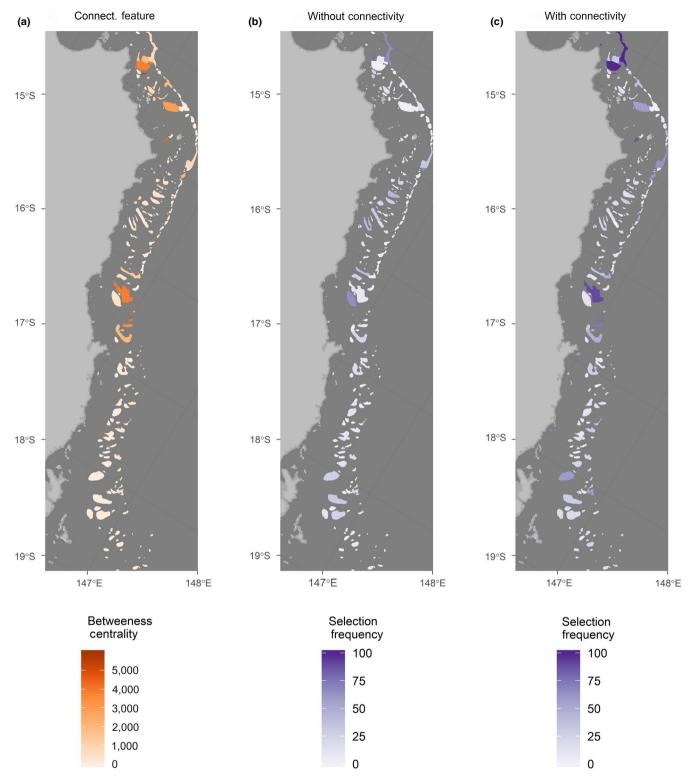


FIGURE 3 Maps of relevant Marxan input and output. Example spatial data from (a) the additional connectivity-based conservation feature (betweenness centrality). The other representation based layers can be found in Figure S1. The resulting Marxan selection frequencies from representation-based Marxan workflow both (b) without and (c) with the added connectivity-based conservation feature

We ran Marxan with and without connectivity (Figure 3b,c) and demonstrate how connectivity influences the spatial distribution of frequently selected planning units (Figure 4). However, it should be noted that incorporating connectivity as features, as we have done in

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this case study, does not guarantee superior conservation outcomes, such as improving population resilience to perturbations or increasing metapopulation viability. This is simply because the value of the connectivity feature was defined a priori using all possible planning units

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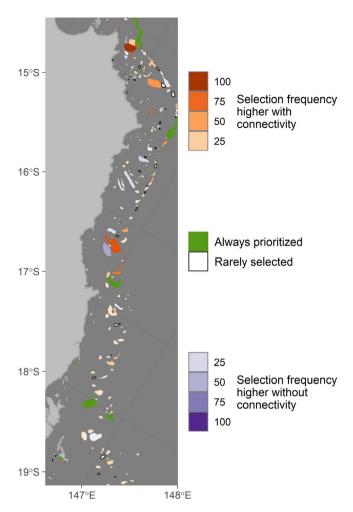


FIGURE 4 The relative difference between the scenarios (positive values indicate planning units that were selected more often with the connectivity added). The "Rarely selected" planning units were selected 5 times or fewer in both cases. The "Always prioritized" planning units were above the 90% percentile for selection in both cases

(i.e., before Marxan analysis), and not re-valued based on those planning units only present in the solution(s). Since realized connectivity can change as a result of protection measures and Marxan connect only accepts static connectivity data, we recommend conducting ecologically meaningful post-hoc testing (e.g. metapopulation modelling; White et al., 2014). Post hoc testing would ideally be conducted for multiple species with varying species traits to evaluate competing strategies, methods, and solutions. We provide an example of how post hoc testing can be conducted in the 'Setting Targets and Post Hoc Evaluation' tutorial (https://marxanconnect.ca/targets.html) on the Marxan Connect website and some post hoc testing capabilities will be added in future versions of Marxan Connect.

6 | CONCLUSIONS

Approaches for including connectivity in spatial prioritization are rapidly evolving but few "best practice" guidelines exist. Connectivity is a

complex topic approached from multiple disciplines and with a diversity of methods that require substantial effort to understand and apply to spatial prioritization scenarios. Here, we present a new open-source tool which offers standardized methods and terminology, builds broad capacity, and helps close the research-implementation gap. Its opensource MIT License (https://github.com/remi-daigle/MarxanConnect/ blob/master/LICENSE) means that it can be modified to meet individual needs and easily updated as best-practices evolve. This combined with the python module, 'marxanconpy' (https://remi-daigle.github.io/marxa nconpy/) (also under MIT License, https://github.com/remi-daigle/marxa nconpy/blob/master/LICENSE), which allows the command line interaction with Marxan Connect functions and the non-proprietary format for the project files (JSON), encourages transparent and reproducible workflows. The approach of targeting conservation features is compatible with other spatial prioritization software. For a user opting to use software such as Zonation (Lehtomäki & Moilanen, 2013), prioritizr (Hanson et al., 2017), or linear programming (Beyer et al., 2018) to identify priorities, there is a high degree of compatibility with Marxan Connect.

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While Marxan Connect represents an advance in facilitating the use of connectivity in the design of protected areas, it does not guarantee that reserves will be "well connected". The practical application of the methods and metrics within Marxan Connect and evaluation by practitioners for effectiveness in their specific planning scenario will enhance its useability. Only post hoc evaluation of the reserve design solution(s) related to ecologically relevant conservation objective(s), such as population viability, expected time to extinction, or metapopulation growth rate, can inform practitioners of the resilience and persistence of targeted populations for a given spatial plan. Similarly, connectivity is only one criterion in planning, and should be considered alongside representation, socio-economic goals, and other species-specific requirements. However, the tools provided in Marxan Connect greatly improve the likelihood that a selected reserve design can adequately meet multiple conservation objective(s).

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AUTHORS' CONTRIBUTIONS

A.M. and M.B. conceived the application and acquired funding; R.M.D. developed the application and website; R.M.D., A.M., A.C.B. and M.B.

worked on the initial development and early testing of the application. All authors made significant contributions to the later development stages of the application and website. All authors contributed critically to making improvements to the application, drafting the manuscript and provided final approval for publication.

DATA AVAILABILITY STATEMENT

The source code for the Marxan Connect software and website can be found at https://github.com/remi-daigle/MarxanConnect and marxanconpy can be found at https://github.com/remi-daigle/marxanconpy. There are repeated references in the tutorial and glossary section of marxanconnect.ca, the website may evolve as the software is improved. The original publication version of the website and app have been archived on Zenodo https://doi.org/10.5281/zenodo.3596175 (Daigle et al., 2019a) and https://doi.org/10.5281/zenodo.3596167 (Daigle et al., 2019b).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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