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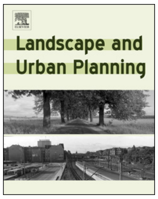

Research Paper

Enhancing conservation network design with graph-theory and a measure of protected area effectiveness: Refining wildlife corridors in Belize, Central America

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ABSTRACT

Maintaining connectivity among remaining natural areas has become increasingly important to ameliorate the negative effects of habitat loss and fragmentation on wildlife populations. Early corridor networks were based on structural connectivity (i.e. habitat structure) and designed to connect protected areas. In recent decades, many methods have been developed to increase the ecological realism of such corridor design to avoid misguided management. However, the multitude and complexity of methods can be a hurdle for conservation planners. Here, we combine a limited set of multiple methods to present a connectivity analysis framework that produces repeatable, intuitive, and ecologically relevant connectivity estimates. We use a modified habitat suitability analysis, accounting for protected area effectiveness, as a starting point for least-cost corridor estimates, and evaluate the network using graph theory. We apply the framework to an existing corridor network in Belize, Central America, by estimating potential functional connectivity for white-lipped peccaries *Tayassu pecari* between systematically identified core patches. We found that forest productivity and protected area effectiveness were important predictors of habitat suitability for white-lipped peccaries. The graph-theoretic network analyses identified particularly important core areas for overall landscape connectivity and indicated potentially weak links in the existing network, while the least-cost corridor outlines indicated general areas where the implementation of connectivity-enhancing measures could strengthen such weak links. With this study, we provide a framework to improve the scientific rigour, ecological meaningfulness, and conservation relevance of applied corridor network design.

1. Introduction

Landscape connectivity is fundamental for maintaining or improving the ecological resilience of landscapes undergoing environmental change (Crooks & Sanjayan, 2006). To maintain landscape connectivity, conservation networks are being established, consisting of natural core areas that are connected through conservation corridors. The corridors are designed to facilitate dispersal between populations and, as such, increase long-term population viability. In the past, the design of conservation networks relied heavily on expert opinion to identify corridors between protected areas by evaluating the structure and orientation of physical landscape characteristics, such as vegetation type and cover, topography, and human disturbance (see examples in Bennett, 2004; Boitani, Falcucci, Maiorano, & Rondinini, 2007).

Under certain circumstances, this approach is still valuable to aid conservation planning, for example where landscape planners do not have access to adequate scientific support (Benedict & Drohan, 2004; Brodie et al., 2014; Correa Ayram, Mendoza, Etter, & Salicrup, 2015; Hoctor, Carr, & Zwick, 2000; Jones, Epps, Mbano, Coppolillo, & Mutayoba, 2007; Sawyer, Epps, & Brashares, 2011; Wangchuk, 2007; Wikramanayake et al., 2004; Zeller, Nijhawan, Salom-Pérez, Potosme, & Hines, 2011). However, a number of limitations have been recognised with this approach. First, the use of expert opinion has been criticised for being subjective and reducing the repeatability and defensibility of landscape connectivity assessments (Chetkiewicz & Boyce, 2009; Rayfield, Fortin, & Fall, 2010; Sawyer et al., 2011). Second, such

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connectivity assessments usually consider only the structure of the landscape, but ideally should consider species characteristics as well as landscape structure, as this generally produces ecologically more meaningful *functional* connectivity estimates (Crooks & Sanjayan, 2006; Magle, Theobald, & Crooks, 2008). In contrast to expert-based structural estimates, such functional connectivity estimates are usually based on species-specific resistance surfaces (Zeller, McGarigal, & Whiteley, 2012), which are parametrised using either species detection data or relocation data tracking actual movements (resulting in potential and actual connectivity estimates, respectively – Fagan & Calabrese, 2006; Rödder, Nekum, Cord, & Engler, 2016). Third, boundaries of protected areas (PAs) often have been used as start and end points for delineating corridors (Belote et al., 2016; Brodie et al., 2014; Zeller et al., 2011). However, some PAs may not hold suitable habitat for the species of conservation concern, and using solely PAs as nodes could exclude potentially suitable areas that are not protected (Beier, Spencer, Baldwin, & McRae, 2011). Additionally, PAs are usually located in sections of the landscape that are not particularly suitable for human activities and are therefore biased towards certain environmental characteristics (Joppa & Pfaff, 2009). Moreover, some PAs provide more protection than others depending on the management effectiveness and the time they have been under protection (Geldmann et al., 2013). Fourth, regardless of how core areas and corridors are defined, the resulting conservation network designs can provide more detailed conservation-relevant information if overall landscape connectivity and the relative importance of each corridor or patch within the network are subsequently quantified. Such assessments are particularly valuable in practical conservation planning, where stringent optimization and prioritization are often necessary due to limited financial resources (Galpern, Manseau, & Fall, 2011).

In the last decade, landscape ecologists and geneticists have worked with conservation planners to devise approaches that avoid one or more of the above limitations. For example, Beier et al. (2011) suggested that defining core areas from a combination of empirically-derived habitat suitability and actual protection status would be more ecologically relevant than using protected area outlines. Landscape genetics (Balkenhol, Cushman, Storfer, & Waits, 2016) and path- or step-selection functions (Benz et al., 2016; Zeller et al., 2016) are increasingly used to provide parameterisations of landscape resistance based on movement and gene flow, but data for these approaches are not always available for species of conservation concern. Least-cost (Adriaensen et al., 2003) and electrical circuit theory (McRae & Beier, 2007) are common ways to identify corridor areas based on reproducible algorithms (Correa Ayram et al., 2015) and can be used even for data-poor species. Similarly, several metrics have been developed to quantify potential functional connectivity provided by identified corridors (Calabrese & Fagan, 2004; Correa Ayram et al., 2015). Specifically, graph-theoretic approaches are commonly used where a network's core areas represent the graph's nodes and its corridors represent edges or links (Fall, Fortin, Manseau, O'Brien, & O'Brien, 2007; Urban & Keitt, 2001). Graph-theoretic approaches have great potential for practical conservation (Zetterberg, Mortberg, Balfors, & Mörtberg, 2010) and have been useful for multi-scale connectivity analyses (Dilts et al., 2016; Tambosi, Martensen, Ribeiro, & Metzger, 2014) or comparing connectivity estimates for different landscape scenarios (Clauzel, Xiqing, Gongsheng, Giraudoux, & Li, 2015; Mimet, Clauzel, & Foltête, 2016). Many of these approaches aim to improve the ecological relevance of conservation network design and to increase repeatability of connectivity estimates, while reducing subjectivity throughout the process. However, the multitude and complexity of these analytical approaches have made their adoption in applied conservation network design slow and cumbersome (Bennett, Crooks, & Sanjayan, 2006; Opdam, Foppen, & Vos, 2002; Resasco, Bruna, Haddad, Banks-Leite, & Margules, 2016).

Here we present and demonstrate an analytical framework that combines a limited set of commonly-used and well-established approaches to provide an ecologically relevant and intuitive approach for corridor network design, including a quantitative evaluation of potential functional connectivity. Our objectives are to present a framework that (i) includes an adequate selection of currently available methods useful for applied conservation planners, (ii) produces more objective and (iii) ecologically more relevant connectivity evaluations than network designs based solely on structural connectivity evaluations between PAs, and (iv) is more informative for conservation planning than either of the individual approaches constituting the framework.

We base our framework on the existing Potential Connectivity Model (PCM) concept by Rödder et al. (2016) and add features that address the limitations mentioned above. For example, we base the PCM on a habitat suitability surface that includes the effectiveness of protected areas as a predictor. This allows us to estimate corridors between core habitat areas as opposed to between PAs, without discounting the effects that PAs have on habitat and movement of the study species. We then estimate least-cost corridors between each pair of adjacent nodes, regardless of the distance between them, and use graph-theory to evaluate the traversability of each suggested corridor, as well as the importance of each node in the network for overall landscape connectivity. To illustrate the framework, we designed a conservation network for an umbrella species (white-lipped peccary *Tayassu pecari*) and compared our network to an existing corridor system in Belize, Central America (Table 1).

2. Methods

2.1. Study area & species

Belize is a small country south of Mexico with over 60% forest cover and 36% of the its terrestrial surface area protected to various extents (Meerman & Roger-Wilson, 2005; but see Young, 2008; Fig. 1). Most of the forest is contained within two major blocks: La Selva Maya and the Maya Mountains (Fig. 1a), which are becoming increasingly isolated due to increasing industrial and small-scale development (Briggs et al., 2013; Radachowsky, Ramos, McNab, Baur, & Kazakov, 2012). Belize also hosts connections between these inland forests and the forests on the Caribbean coast (Fig. 1b). All connections are negatively affected by habitat destruction and fragmentation (Briggs et al., 2013; Meerman & Roger-Wilson, 2005).

We chose Belize for our study because within the country, a current set of corridors already has been suggested between blocks of PAs (BERDS, 2005; Meerman, 2000; Petracca, 2010; Wildtracks, 2013), which are used as reference throughout the study (Fig. 1b). The delineation of these corridors has been based primarily on structural connectivity. Since functional connectivity estimates require a species-specific approach, in this study, we use our framework to design a corridor network for an umbrella species (Breckheimer et al., 2014). The white-lipped peccary (*Tayassu pecari*) is a gregarious ungulate (VU – IUCN, 2017) that usually travels in herds (sounders) of up to 300

Table 1
Characteristics of the currently suggested biological corridors in Belize and the Potential Connectivity Model developed in this study.

	Current corridors*	Presented model
Habitat suitability model	Expert opinion	Environmental variables + PA effectiveness & Maximum Entropy modelling
Nodes	Protected areas	High-suitability areas
Connectivity type	Structural/Functional	Functional (Potential)
Connectivity model	Expert opinion/Least-cost	Least-cost + graph-theory

* (BERDS, 2005; Meerman, 2000; Petracca, 2010; Wildtracks, 2013).