Ecological Indicators 158 (2024) 111387

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Original Articles

Percentage of area protected can substitute for more complicated structural metrics when monitoring protected area connectivity

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A R T I C L E I N F O

Keywords:
Landscape metrics
30x30
Landscape ecology
Connectedness
Convention on Biological Diversity
Landscape management
Conservation

A B S T R A C T

Protected area (PA) targets have become a hallmark of global conservation policies such as the recent Kunming-Montreal Global Biodiversity Framework, which requires signatory countries to establish new PAs while also monitoring gains to both PA network coverage and connectivity at large spatial scales. Policy makers tasked with implementing and monitoring progress toward these targets face the difficult decision about which connectivity metric to use, which is not always straightforward given existing data and software limitations. We empirically compare 17 of the most widely used structural connectivity metrics to determine how they capture change in a PA network as additional protected areas are added and assess whether mathematically simple metrics are a reasonable substitute for more complex metrics. We find that simply reporting the percentage of the total area that is protected is a viable way to capture connectivity gains in most landscapes. If a more involved metric is desired, we recommend the Integral Index of Connectivity, which was highly correlated with the percentage of area protected, produced similar results when measuring change in PA networks, and incorporates stepping stone movements through transboundary regions.

1. Introduction

Biodiversity loss is a global concern as more than a million species are at risk of extinction (Tollefson. 2019). Habitat fragmentation and loss is driving much of this extinction risk (Laita et al., 2011; Zahler and Rosen, 2013). On average, species have lost an estimated 18 % of their home range sizes to land cover change and other anthropogenic factors, with future losses projected to reach 23 % by 2100 (Beyer and Manica, 2020). As species' home ranges become fragmented and degraded by development while also shifting due to climate change, it is imperative to ensure that remaining habitat areas are connected to facilitate movement, dispersal, and gene flow (Beger et al., 2022; Gilbert-Norton et al., 2010; Rudnick et al., 2012).

Protected areas (PAs) are a key mechanism for managing land use and conserving biodiversity (Saura et al., 2017) and are a fundamental component of area-based conservation efforts (Maxwell et al., 2020). PA targets have become a hallmark of global conservation policies including the Convention on Biodiversity (CBD). For example, the recent Kunming-Montreal Global Biodiversity Framework aims to protect at least 30 % of terrestrial land and water by 2030 through well-connected and ecologically representative PAs (CBD, 2022). While the '30x30′ area target is the centerpiece of this framework, evaluating the degree to which PA networks are connected is also of major policy importance (Naidoo and Brennan, 2019). Satisfying these goals will require countries to not only establish new protected areas but also monitor gains to PA network coverage and connectivity at large spatial scales.

Connectivity, which can be defined as the degree to which a landscape facilitates or impedes the flow of ecological processes including the movement of organisms (Kindlmann and Burel, 2008; Taylor et al., 1993; Unnithan Kumar and Cushman, 2022), encompasses ecological processes such as gene flow, energy transfer, and climate migration at different organizational levels and across spatio-temporal scales (Beger et al., 2022). Connectivity has been widely studied in ecology and landscape ecology over the past several decades (Correa Ayram et al., 2016; Prugh, 2009), and more than 40 different spatial metrics have been developed to measure connectivity in landscapes (Keeley et al., 2021; Rayfield et al., 2011). These metrics vary in their theoretical basis (e.g., patch-based, graph theory, circuit theory), mathematical formulations, data requirements, and computational complexity, which has led to wide variation in adoption. Furthermore, new connectivity

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https://doi.org/10.1016/j.ecolind.2023.111387
Received 26 July 2023; Received in revised form 10 November 2023; Accepted 3 December 2023
Available online 9 December 2023

metrics are constantly being developed (e.g., Fletcher et al., 2019; Petsas et al., 2021; Van Moorter et al. 2022; Theobald et al. 2022), with data inputs and mathematical involvement often growing with each iteration.

Despite the large number and variety of metrics, little guidance exists on how to select an appropriate metric, particularly in the context of global conservation targets, which will require shared reporting frameworks amongst participating nations (Theobald et al. 2022). Policy makers tasked with implementing and monitoring these global targets thus face the difficult decision about which connectivity metric to use and how to operationalize it, which is not always straightforward given the data and software limitations that exist for some areas. While there have been several conceptual reviews of connectivity metrics in the past (Calabrese and Fagan, 2004; Keeley et al., 2021; Kindlmann and Burel, 2008; Rayfield et al., 2011; Unnithan Kumar and Cushman, 2022), there is a lack of empirical comparisons establishing which metrics are analogous and whether certain metrics provide unique information about landscape connectivity that should be considered. This information would benefit decision makers tasked with monitoring and reporting progress toward global and local conservation targets, often with limited resources.

This study contributes an empirical comparison of 17 of the most widely used structural connectivity metrics in the context of increasing protected area networks to meet global conservation targets. First, we deconstruct the equations of the 17 metrics according to their mathematical structure. Based on those structures, we develop a typology that can be used to guide metric selection by considering what components of the PA network each metric is capturing. Next, we simulate changes in three, existing PA networks to compare how the 17 metrics capture network change. We use this comparison to assess whether mathematically simple metrics can reasonably substitute for more complex metrics when measuring change in PA connectivity. Finally, we discuss the implications of our findings for monitoring progress toward area-based conservation goals.

2. Materials and methods

2.1. Metric selection and categorization

We selected 17 commonly-used structural connectivity metrics from a comprehensive list compiled from a literature review (Correa Ayram et al., 2016; Keeley et al., 2021; Laita et al., 2011; Pascual-Hortal and Saura. 2006; Prugh, 2009). We retained metrics with more than 100 citations (Google Scholar) and omitted metrics that have been shown to respond abnormally to increases in protected area (Pascual-Hortal and Saura, 2006). While functional connectivity is critical for species-specific conservation activities, structural connectivity can provide a general assessment of landscape connectivity to support strategic network planning for multiple ecosystem services (Butler et al., 2022; Minor and Urban, 2008; Rieb and Bennett, 2020). Similarly, we did not consider resistance-based metrics because they often require target species, and our overarching goal is to identify metrics that can support general conservation targets that cover a range of species. There is also a lack of general consensus on the optimal method for constructing resistance surfaces (Zeller et al., 2012), and these surfaces can be difficult to compute in data sparse regions. Lastly, resistance-based methods do not have the same interpretability and reporting suitability as structural metrics, and often require summarization such as taking the median value within an administrative area of interest (Van Moorter et al. 2022; Harwood et al., 2022; Brennan et al., 2022).

The final list of 17 structural metrics includes: the percentage of the study area that is protected (*PctArea*, akin to *Prot* in Saura et al. (2017)), Patch Cohesion Index (*Cohesion*), distance to the nearest neighbor patch (*Dist*), mean radius of gyration (*Gyrate*), area-weighted mean radius of gyration (*AWGyrate*), area of habitat within buffer (*BA*), flux (*Flux*), area-weighted flux (*AWF*), Equivalent Connected Area (*ECA*), Probability of Connectivity (*PC*), Proximity Index (*Prox*), Betweenness Centrality (*BC*), node degree (*Degree*), clustering coefficient (*ClusCoeff*), compartmentalization (*Compart*), Integral Index of Connectivity (*IIC*), and Protected-Connected Index (*ProtConn*). Metrics were computed as global statistics at the class level using R (version 4.0.0). Full equations for each metric with explanations and references are provided in the Supplemental Material (Appendix A).

We deconstructed each metric according to its mathematical components (e.g., area, distance terms, graph components) and systematically categorized those components to permit an algorithmic structure comparison across metrics. In contrast to conceptual reviews (Kindlmann and Burel, 2008; Keeley et al., 2021), we coded each metric according to its structural components and created groups of structurally and mathematically similar metrics. These groups provide a basis for assessing the mathematical equivalency of different metrics and ultimately determining whether certain metrics overlap in how they measure connectivity, which can potentially offer guidance into which metrics may be better suited for reporting and monitoring.

2.2. Experimental design to compare change in connectivity with PA expansion

A key component of ongoing global biodiversity monitoring is measuring gains in network connectivity as PAs are added to the network. Since it is not possible to predict where future PAs will be sited, we developed an approach to capture connectivity changes in network expansion by simulating the addition of protected areas from within the existing PA network. We first selected three study areas (California, USA; Colombia; and Liberia) with different land management policies, histories of protected area gazetting, and PA network composition and configuration to test how the metrics performed across different systems (Fig. 1). California, located in the western US and bordering Mexico to the south and the Pacific Ocean to the west, is rich in biodiversity, with 13 ecoregions across 4 biomes. About 15 % of the natural land of California is identified as climate refugia for plants (Thorne et al., 2020). Colombia, located in South America and bordering the Caribbean Sea, the Pacific Ocean, and the countries of Panama, Venezuela, Ecuador, Peru, and Brazil, is the second most biologically diverse country in the world and has been protecting land for almost 30 years. Liberia, located in Africa and bordering Sierra Leone, Guinea, the Ivory Coast, and the Atlantic Ocean, is also a global biodiversity hotspot but has been suffering from degradation of important ecosystems such as mangroves, wetlands, and forests (De Sousa et al., 2023).

For each study area, we constructed a PA database that includes all terrestrial PAs including those within a distance of 230 km beyond the study area boundary (for stepping stone analyses). Data for California and other states in the US were gathered from the Protected Areas Database of the United States (PAD-US 2.0, USGS, 2018), and we retained terrestrial PAs managed for biodiversity (GAP status 1 or 2). We removed patches smaller than 1 km^2 to reduce processing time, resulting in 1,151 terrestrial PAs covering almost 96,000 km^2 that vary in size. Data for Colombia and surrounding areas were gathered from the World Database on Protected Areas (WDPA, UNEP-WCMC & IUCN, 2021), and we similarly removed small patches and simplified vector boundaries using a 50 m tolerance to reduce complexity, resulting in 394 terrestrial PAs covering more than 193,000 km^2. Data for Liberia were obtained from local sources that reflect a more up-to-date network than WDPA, but surrounding data were obtained from the WDPA. Liberia recently expanded their PA system to include 16 areas to better protect endemic and endangered species (Frazier et al., 2021a). All three networks were processed following Saura et al. (2019) and rasterized at 1 km resolution. We coded the 17 metrics in R (see Supplemental Material for details) and computed all metrics at the class level. For metrics requiring a 'search distance' or median dispersal distance, we used 10 km, which is a median value established in the literature for dispersal distances of mammals (Bowman et al., 2002; Minor and Lookingbill, 2010) and is

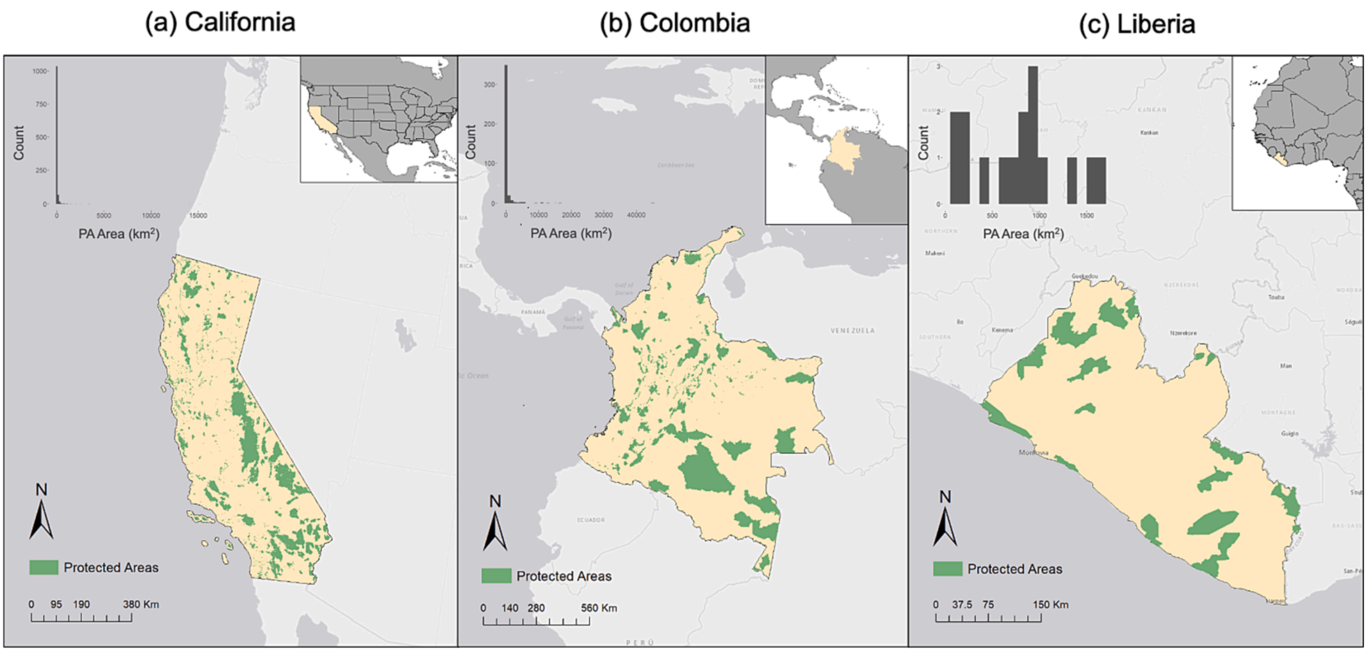

Fig. 1. Protected area networks and study area boundaries for (a) California, (b) Colombia, and (c) Liberia. Histograms at the top left corners show protected area size distributions.

sufficient for providing a basis for demonstration and comparison given that metrics often scale linearly with these distances.

We simulated the addition of protected areas to the networks through an inverted approach, where we randomly dropped 10 % of the total number of PAs in each network and analyzed the percent change in connectivity between the simulated base network and the expanded network (Eq. (1)).

$$\%Change = 100 \times \frac{Metric_{expanded} - Metric_{base}}{Metric_{base}} \tag{1}$$

We repeated this process of dropping 10 % of PA patches 100 times to produce a distribution of connectivity changes. Since Liberia only contains 16 PAs, for each iteration we removed two patches and ran all 120 possible iterations.

We conducted a set of analyses to identify statistical similarities in how the 17 metrics measured connectivity change. First, we used summary statistics to identify whether any metrics produced anomalous or unexpected measures of connectivity change (e.g., reduced connectivity with network expansion). Second, we normalized metric values and used Pearson's correlation analysis and Principal Component Analysis (PCA) to determine which metrics measured connectivity change in strongly related ways. Third, we created ridgeline plots of the connectivity change distributions to visually examine similarities in how metrics capture network change. Lastly, for each metric pairing, we also plotted the proportion of distributions for which those metrics exhibited similar levels of change.

3. Results

3.1. Metric typology

We identified eight mathematical elements characterizing the 17 connectivity metrics (Table 1). These eight elements can be grouped into three general categories of physical components, graph components, and ecological components (Table 1) that together cover aspects of both the composition and configuration of the network. Physical components

Table 1
Metric typology based on mathematical deconstruction of 17 connectivity metrics. The typology classifies metrics into three types: metrics that contain only physical components (Type 1), metrics that contain graph components (Type 2), and metrics that contain an ecological component (Type 3).

		Physical Components				Graph Components			Ecological Component
	Metric	Area	Distance	Threshold	Perimeter	Node	Link	Path	Distance Decay
Type 1	Percentage of area (*PctArea*)	✓							
	Patch Cohesion Index (*Cohesion*)	✓			✓				
	Distance to the nearest neighbor patch (*Dist*)		✓						
	Mean radius of gyration (*Gyrate*)	✓	✓						
	Area-weighted mean radius of gyration (*AWGyrate*)	✓	✓						
	Area of habitat within buffer (*BA*)	✓		✓					
	Proximity index (*Prox*)	✓	✓	✓					
Type 2	Betweenness Centrality (*BC*)			✓		✓		✓	
	Node degree (*Degree*)			✓		✓	✓		
	Clustering Coefficient (*ClusCoeff*)			✓		✓	✓		
	Compartmentalization (*Compart*)			✓		✓	✓		
	Integral Index of Connectivity (*IIC*)	✓		✓			✓		
Type 3	Flux (*Flux*)		✓						✓
	Area-weighted flux (*AWF*)	✓	✓						✓
	Equivalent Connected Area (*ECA*)	✓	✓						✓
	Probability of Connectivity (*PC*)	✓	✓						✓
	Protected-Connected Indicator (*ProtConn*)	✓	✓						✓

are the most basic structural characteristics and include elements such as the area of patches and the distances between them. Graph components refer to the various elements of a graph of protected areas that are relevant to connectivity such as the number of nodes (patches), links (direct connections between nodes), and paths (sequences of links connecting nodes). The single ecological component we identified in the set of metrics (distance decay) represents the mathematical abstraction of ecological assumptions on species dispersal.

The four elements comprising the physical components are area, distance, threshold distance, and perimeter (Table 1). All of the 17 metrics contain at least one of these four elements. Area, represented in 11 of the 17 metrics, captures the size of individual PAs in the network. Distance, represented in nine metrics, captures how close PAs are to one another. Threshold distance, represented in seven metrics, captures a search distance within which other structural factors are considered, such as the number of patches or links. Perimeter, represented in a single metric (*Cohesion*) has implications for connectivity in terms of patch accessibility.

We identified three graph components in the metrics we examined: counts of nodes, links, and paths. While many metrics are conceptualized based on graph theory, the graph components we identify here are explicitly included in the metric equation. Nodes are point representations, usually of habitat patches, links are the direct connections among nodes within an established distance threshold, and paths are a series of links that connect a pair of nodes. Links represent direct inter-patch dispersal activities whereas paths also account for connectivity using stepping-stones. Graph components are always used in combination with a threshold distance to characterize a cutoff point within which the number of nodes, links, and paths are tallied. Five metrics include explicit counts of graph components in their equations, with *Degree*, *ClustCoeff*, and *Compart* including counts of nodes and links, *BC* including counts of nodes and paths, and *IIC* including counts of links.

The only element in the ecological component category is a distance decay function, which is frequently included in connectivity metrics to capture species dispersal and functional connectivity. Five of 17 metrics include a distance decay component, which typically takes the following form:

$$p_{ij} = e^{(-\theta \bullet d_{ij})} \tag{2}$$

$$\theta = -ln(0.5)/r \tag{3}$$

where the probability of dispersal, p_{ij}, between PAs i and j, is represented by a negative exponential function, d_{ij} , which is the distance between PAs i and j, and θ is a function of the median dispersal distance r such that the probability of dispersal is 50 % when the distance between two PAs equals r (Saura et al., 2018).

In general, Type 1 comprises the most mathematically simple metrics that include only physical components. Type 2 comprises metrics that include some physical component(s) and at least one graph component in their equation. These metrics also often only require few, if any, user-defined values such as a distance threshold to define neighbors, and they are relatively easy to compute. Type 3 comprises metrics that include an ecological component in the form of a distance decay function. This group of metrics is the most complicated to implement because they require user-specified inputs for the median dispersal distance that would ideally match species movement patterns.

3.2. Metric operationalization

The 17 metrics have similar data requirements but vary greatly in terms of value ranges and metric units (Supplemental Material, Appendix B), which can complicate their comparison and interpretability. Metrics that are mathematically bounded with a fixed value range (e.g., 0 to 1) and those with a measurement unit that is clearly associated with ecological meaning (e.g., km^2) are preferred because they are easier to interpret (Kedron et al., 2018; Li and Wu, 2004; Saura and Pascual-Hortal, 2007) and are therefore more straightforward to use in policy reporting. Ten metrics have a fixed maximum value (Appendix B), but only three metrics can be interpreted as area or percentage of area (i.e., *PctArea*, *ECA*, and *ProtConn*).

All of the metrics can be programmed in R, which may help reduce technological barriers to uptake, but some are more computationally complex than others, particularly the Type 3 metrics that have a distance decay function. The R package 'Makurhini' (Godínez-Gómez, O. and Correa Ayram, 2020) greatly improves the computation speed for these metrics by introducing optional parallel processing. There is also a growing user community focused on improving computational efficiency through the Julia programming language (Hall et al., 2021; Landau et al., 2021; Van Moorter et al. 2022; Anantharaman et al., 2020).

3.3. Metric correlations

A majority of the metrics exhibited strong, positive correlations when measuring change in network connectivity (Fig. 2). These metrics include *Gyrate*, *Cohesion*, *AWGyrate*, *AWF*, *IIC*, *PC*, *ECA*, *ProtConn*, and *PctArea*, as well as *BA* and *BC* in California. This set of highly correlated metrics persists across the three study regions, suggesting that the relationships are driven by mathematical similarities and are generalizable across locations, although Liberia shows only moderate correlation for *AWGyrate*. We also observe high correlation between *Flux* and *Degree* in all three study areas despite these metrics not sharing any mathematical components (Table 1). Conceptually, these two metrics are both influenced by the patches in the immediate neighborhood, and their correspondence supports the potential to substitute a mathematically simpler metric, *Degree*, which sets a threshold distance for neighborhood, for a more complex metric, *Flux*, which uses a distance decay function that requires additional parameterization to account for species movement.

The PCA results (Table 2) largely support the Pearson's correlation results with PC1 loaded heavily with the same set of correlated metrics in all three study regions. Each of these metrics includes area in their equation (Table 1), and thus PC1 emphasizes landscape composition. The only metric with an area term that does not load highly on PC1 is *Prox*, which is the most involved of the Type 1 metrics because it includes area, distance, and threshold distance in its equation. *BA,* which also includes area and threshold distance, only loaded heavily on PC1 in California. Both PC2 and PC3 show more variation in the metric loadings, while still supporting the same general findings from the Pearson's correlation. *Flux* and *Degree*, which were highly correlated (Fig. 2), both loaded consistently on PC2 in all three regions (Table 2). Metrics loading highly on PC3 vary across the three sites, however for each site, they comprise measures of distance, which suggests PC3 is also capturing distance and configuration.

3.4. Metric responses to changing PA networks

For reporting purposes, connectivity metrics should be simple to interpret and their values should be affected in the same direction as PAs are added to the network. In other words, increases in area conserved should not result in a decrease in connectivity, regardless of how the metric measures change. While more complex metrics measuring subtle, ecologically specific features of connectivity may rise or fall with additions to a PA network, this variation complicates interpretation. For generalizable and comparable reporting frameworks, metrics with consistent directional changes are preferred. We identified nine metrics that exhibited inconsistent directional changes as PAs were added to the three networks (Supplemental Material, Appendix C). These metrics include *Prox*, *Compart*, *ClustCoeff*, *Degree*, *Cohesion*, *Gyrate*, *BC*, *BA*, and *AWGyrate*. We advise that these metrics are suboptimal for general global target reporting and should be avoided as they may result in

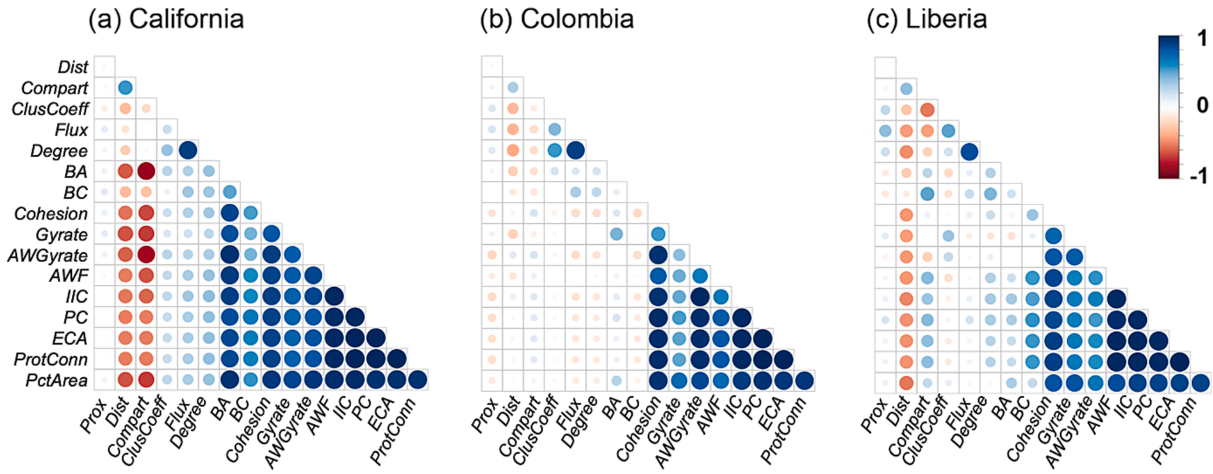

Fig. 2. Pair-wise Pearson's correlation matrix for all 17 metrics in (a) California, (b) Colombia, and (c) Liberia. Larger circles indicate higher significance, with color also indicating the degree of correlation.

confusion amongst reporting entities and may lead organizations to exclude otherwise valuable areas because they might aberrantly decrease connectivity.

Distributional plots of the percent change of each metric between the expanded and simulated base PA networks show that there is a high degree of similarity across metrics in terms of how they capture connectivity change as PAs are added to the network (Fig. 3). Most metrics have a dominant, Gaussian peak centered at low levels of percent change (near zero), and several have a secondary, or even tertiary, peak in the right tail. These secondary peaks are most pronounced in the set of metrics that were found to be highly correlated (Fig. 2) and loaded together on the first principal component (Fig. 3), which all shared a measure of area in their equation. A small number of metrics exhibited more uniform distributions, including *BC* in California and Colombia and *Dist* and *AWF* in Liberia. Uniformity in the distribution of these metrics may indicate that they are more sensitive to small changes in the PA network compared to other metrics.

Given the visual similarities between the distributions for the mathematically simpler metrics, like *PctArea*, and more mathematically involved metrics, like *ProtConn* and *ECA*, we empirically assessed pairwise similarities by calculating the absolute difference in the percentage change in connectivity for each simulation. This approach controls for variation in how metrics may measure change across simulations, which may be masked when amassed in a distribution plot. This calculation produced 100 absolute differences for each of the 136 metric pairings in California and Colombia and 120 absolute differences for metric pairings in Liberia. We plotted the cumulative absolute difference functions for *PctArea* and *Dist*—the two simplest metrics in terms of their mathematical components (Table 1)—against metrics identified as having high similarity in the Pearon's and PCA analyses and distributions of percent changes to illustrate how these simpler metrics often produce measures of connectivity change that are very similar to the more mathematically involved metrics. In these comparison plots (Fig. 4), the horizontal axis indicates the absolute difference in the percent change in network connectivity between *PctArea* or *Dist* and the metric to which they are paired. Smaller values on this axis indicate smaller absolute differences and, therefore, greater similarities in how the two metrics measure connectivity change. The vertical axis indicates the percent of simulations that meet a given level of absolute difference. Smaller values on this axis indicate lower counts of simulations. We include a visual reference in the plots along the vertical axis at 50 % to facilitate identification of the level of absolute difference that half the simulations fall under.

Metric pairs that exhibit a steep rise up to 100 % on the vertical axis at low absolute differences on the horizontal axis indicate high similarity and the potential for direct substitution when measuring connectivity change. An example of this pattern is the pairing of *PctArea* and *ProtConn* in all three regions (Fig. 4a). Cases where a steep rise is delayed until higher levels of absolute differences further along on the horizontal axis indicate the metrics are related, but they may not be full proxies. An example of this pattern is *Flux* and *Dist* for California and Colombia (Fig. 4b). Metric pairs that rise more shallowly indicate less similarity, and substitution is not recommended. An example of this is the pairing of *AWF* and *PctArea* in California and Liberia (Fig. 4a). Metrics that plateau below 100 percent indicate that certain patterns of network change will spur large differences in the metrics. An example is *AWF* paired with *PctArea* in Colombia where for about 75 percent of simulations the differences are quite small, but in certain network configurations, the differences are very large, indicating that substitution is not recommended.

In summary, the results confirm that *PctArea* is consistently similar to five metrics (*BA*, *ECA*, *IIC*, *PC*, *ProtConn*) in measuring changes in network connectivity (Fig. 4a) with the majority of simulations having differences of less than 10 percent. This pattern is consistently observed in California and Colombia, with *BA* having more differences in Liberia, likely due to its small number of PAs, which suggests that *PctArea* is a viable and easy-to-compute substitute for these more involved measures. We similarly confirm that *Dist* is consistently similar to five metrics (*Cohesion*, *Compart*, *Degree*, *Flux*, *Gyrate*).

4. Discussion

The 30x30 target in the Kunming-Montreal Global Biodiversity Framework has become a benchmark for global conservation efforts, but implementing it will require a shared reporting and assessment framework for signatory countries to communicate their progress. Monitoring gains to connectivity at large spatial scales is complicated by the plethora of available metrics, some of which require involved analyses and sophisticated data, along with the limited guidance available on which metrics are best suited for different situations. Furthermore, many existing metrics are challenging to implement and interpret, which could create reporting or communication burdens and lead to a lack of disclosure surrounding conservation gains. To assist with identifying metrics for monitoring gains in PA network connectivity, we empirically compared 17 of the most widely used structural connectivity metrics to determine whether a simple metric may be suitable for reporting connectivity change.

The main finding we identified is that simply reporting the area percentage of land protected is a viable way to capture connectivity gains associated with general PA network expansion. While more

Table 2
Principal component analysis results for the first three components derived for California, Colombia, and Liberia. Values are metric loadings for each principal component (PC) represented by eigenvectors. Values greater than 0.25 are bolded. Percentage of variance captured by each component is provided in brackets.

	Prox	*Dist*	*Compart*	*ClusCoef*	*Flux*	*Deg*	*Gyrate*	*BC*	*Cohesion*	*BA*	*AWGyr*	*AWF*	*IIC*	*PC*	*ECA*	*ProtConn*	*PctArea*
California																	
PC1 (62.1 %)	−0.02	0.20	0.22	−0.09	−0.11	−0.13	**−0.26**	−0.19	**−0.29**	**−0.29**	**−0.28**	**−0.30**	**−0.30**	**−0.29**	**−0.29**	**−0.29**	**−0.30**
PC2 (10.9 %)	−0.06	−0.07	**−0.3**	−0.21	**−0.63**	**−0.62**	0.14	−0.15	0.06	−0.09	0.11	0.02	0.00	0.01	0.06	0.06	0.05
PC3 (6.95 %)	**−0.35**	**−0.36**	**−0.27**	**0.67**	0.02	0.11	0.03	**−0.33**	−0.05	0.1	0.12	−0.09	−0.09	−0.15	−0.14	−0.14	−0.02
Colombia																	
PC1 (45.5 %)	0.07	−0.01	−0.05	0.02	0.07	0.06	−0.21	0.05	**−0.35**	−0.05	**−0.34**	**−0.28**	**−0.35**	**−0.36**	**−0.35**	**−0.35**	**−0.34**
PC2 (16.6 %)	−0.10	**0.39**	0.22	**−0.38**	**−0.49**	**−0.51**	−0.19	−0.20	0.01	**−0.26**	0.05	−0.09	0.01	−0.03	−0.02	−0.02	−0.07
PC3 (7.84 %)	−0.16	−0.23	**−0.40**	**−0.25**	**−0.29**	**−0.31**	**0.41**	0.09	−0.02	**0.53**	−0.16	−0.04	−0.08	−0.04	−0.10	−0.10	0.11
Liberia																	
PC1 (48.3 %)	−0.03	0.19	−0.10	0.00	−0.04	−0.11	**−0.25**	−0.17	**−0.32**	−0.08	−0.24	**−0.34**	**−0.34**	**−0.34**	**−0.34**	**−0.34**	**−0.32**
PC2 (16.6 %)	−0.18	**0.33**	**0.49**	**−0.45**	**−0.47**	**−0.34**	−0.08	0.13	−0.04	0.07	−0.15	0.10	0.05	0.04	0.08	0.08	0.02
PC3 (13.3 %)	0.10	0.02	−0.2	0.16	**−0.35**	**−0.46**	**−0.39**	**−0.39**	0.15	**−0.33**	**0.34**	−0.05	−0.05	−0.10	−0.04	−0.04	0.16

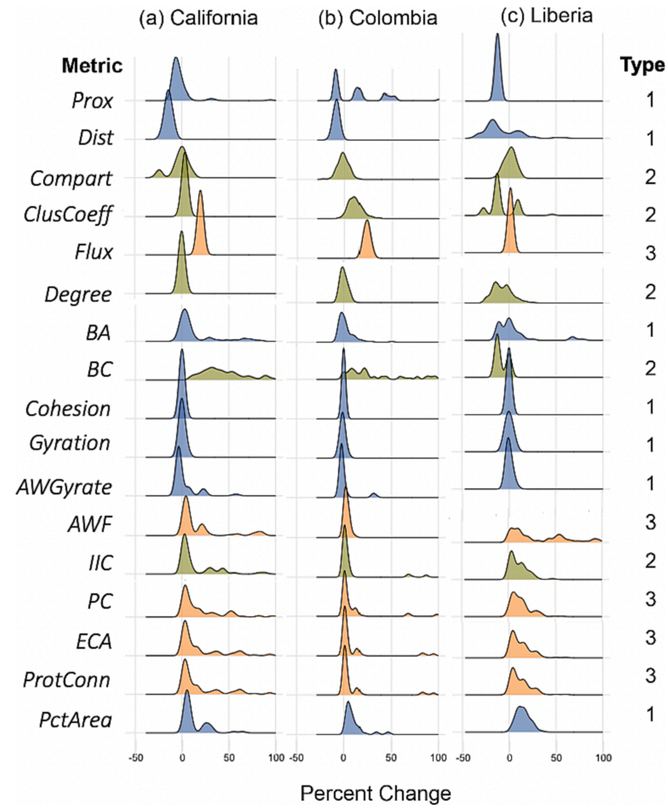

Fig. 3. Ridgeline plots of percent changes in values of the 17 metrics between the simulated base and expanded PA networks for the three study areas. Blue, green, and orange represent Type 1, 2, and 3 metrics (Table 1), respectively. Values are included up to 100% change.

complex metrics that measure finer nuances of landscape composition and configuration are valuable in many situations, we found that the metric *PctArea*, which is simply the percent of the landscape that is protected, was a suitable proxy and captured connectivity change in much the same way as the more mathematically involved metrics. This finding has implications for both science and policy. From a policy standpoint, using a metric based on a straightforward concept like ‘the percentage of area protected’ can facilitate communication with diverse and non-technical audiences while also lowering the costs of measuring and reporting progress. If a more complex structural metric is desired, we recommend the Integral Index of Connectivity (*IIC*; Pascual-Hortal and Saura, 2006), which was highly correlated with *PctArea* and produced similar results when measuring change in PA networks. *IIC* incorporates stepping stone movements through dispersal distance, but it does not use a distance decay function that defines some of the more complicated metrics like Equivalent Connected Area (*ECA*) or Protected Connected Index (*ProtConn*).

Scientifically, our findings show that area is the dominant driver of many structural connectivity metrics and is central to how these metrics measure change in network connectivity. This finding is evidenced by the high correlation coefficients between *PctArea* and eight other metrics (Fig. 2), which were generally above 0.8. These same nine metrics also loaded together on the first component of the principal component analysis (Table 2), indicating that most of the variance in connectivity change can be explained by these area-dominated metrics. In contrast, metrics that did not include an area component were less correlated and showed fewer similarities in how they measured connectivity change. The finding that *PctArea* is a sufficient metric to measure changes in structural connectivity is logical since higher connectivity is associated with larger areas, particularly given the positive associations between biodiversity and patch size (Chase et al., 2020; Connor and McCoy,

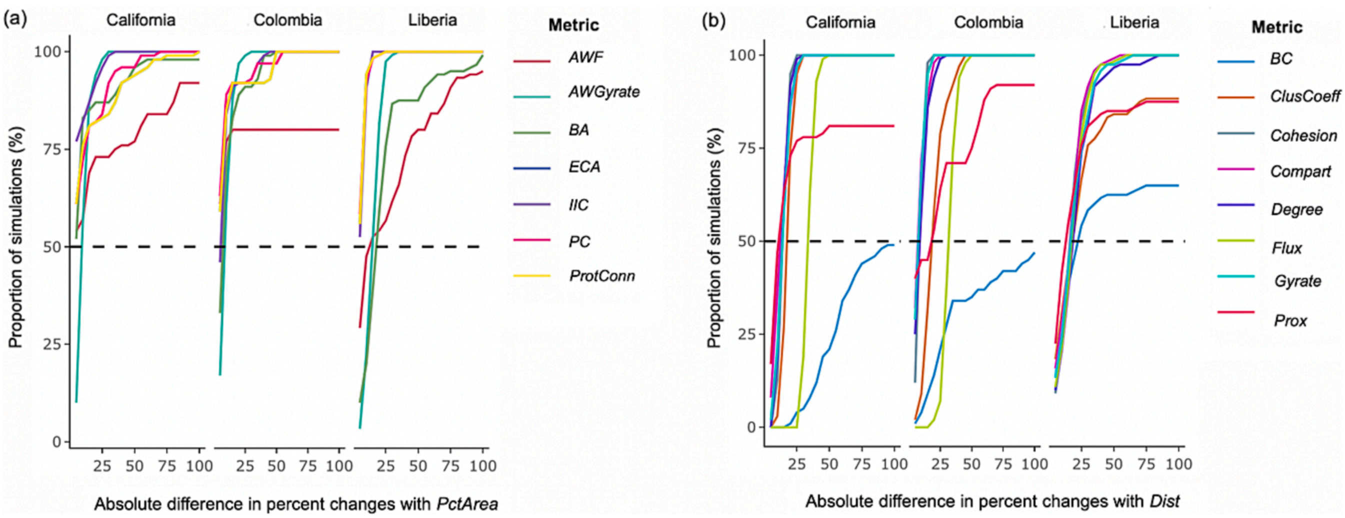

Fig. 4. Similarity in metric pairings measured by the cumulative percentage of simulations meeting varying levels of absolute difference in the connectivity change. Pairwise comparisons between (a) *PctArea*, (b) *Dist,* and correlated metrics.

1979; Hodgson et al., 2010). In many cases, the total area protected will also indirectly impact the second primary component of most connectivity metrics–the distance between PAs.

While our findings confirm that there is redundancy among connectivity metrics (Ritters et al. 1995; Hughes et al., 2023), we also found that metrics and the relationships among them are sensitive to differences in the composition and configuration of the network. In general, results in Liberia sometimes diverged from those in California and Colombia, which may be due to Liberia's PA network being much smaller compared to California or Colombia. Liberia's protected areas are also more uniform in size, as there are very few small patches, whereas California and Colombia have larger numbers of relatively small protected areas. Moreover, we found that certain metrics may be more sensitive than others to the addition of PAs and to overall network configuration. For example, in Liberia, where there were fewer PAs, the Betweenness Centrality (*BC*) changed less over the simulations than in California and Colombia where the networks are larger, resulting in flatter histograms (Fig. 3).

Our work opens several paths for researchers interested in connectivity metrics and area-based conservation. First, future studies should examine how to incorporate time and incremental PA network change into connectivity monitoring for conservation. In this study, we examined a simple two-step representation of a relatively large, 10 % expansion of a PA network. However, efforts to expand PA networks are more likely to unfold slowly and incrementally as PAs are added individually or in small groups. This reality makes understanding the dynamics of incremental change essential to 30x30 conservation efforts. Our findings are an important first step in this direction. For example, we identified metrics that produce positive and negative measures of connectivity change when a PA network is expanding. These metrics may oscillate as PA networks slowly grow, potentially signaling to observers that conservation efforts are not producing desired results, which could reduce support for future plans to protect other areas. This possibility further supports our suggested use of simple metrics like *PctArea* that move uniformly with network expansion and directly relate to the central formulation to 30x30 targets.

Second, our analysis focused only on the presence of protected areas and did not consider the quality of the underlying landscape or the effectiveness of these areas for facilitating animal movement or achieving specific biodiversity or ecosystem functioning goals. The literature is clear that protected areas vary in their effectiveness for achieving conservation goals (Le Saout et al., 2013; Watson et al., 2014). Furthermore, ignoring the underlying landscape heterogeneity and vulnerability to human degradation can lead to misassessment of PA connectivity (Naidoo and Brennan 2019). Landscape resistance surfaces and associated metrics can help overcome these limitations, and when possible, more detailed analyses are certainly encouraged to determine PA effectiveness and where to site future Pas to optimize functional connectivity. However, for standardized, global reporting, there is value in having simple and easy to interpret metrics that utilize the same input data and can provide overall comparisons in many situations. Similarly, moving forward, biodiversity targets and increases to the protected area network will also need to consider how climate change might compromise the functioning of these areas (Arneth et al., 2020). Structural connectivity metrics cannot account for landscape dynamism, and more research in general is needed to understand the ecological and situational relevance of metrics (Vicente et al., 2022).

Lastly, our analysis did not test metric sensitivity to changing spatial scales. Habitat connectivity is scale dependent (Cushman et al., 2016), and so it is critical to address scale explicitly in studies using landscape metrics to assess connectivity (Ciudad et al., 2021; Frazier et al., 2021b; Frazier and Kedron, 2017; Wu, 2004). Correlations between metrics may be higher at smaller spatial scales (Hughes et al., 2023), and so careful attention should be given to the analysis scale. We rasterized protected areas at a 1 km scale, which was appropriate given the size of the study areas and considerations for compute time. However, there may be areas where smaller or larger resolutions are appropriate. When raster data are used to assess and monitor progress toward global targets, we recommend standardizing the resolution across countries so that metrics, including area, can be compared.

In summary, we developed a typology of structural connectivity metrics based on their mathematical components and empirically compared them to assess how they respond to protected area network expansion. The results of the empirical simulations suggest information redundancy exists in the set of structural metrics used to measure protected area network connectivity, and that area drives much of the variation. To that end, we found that simpler metrics including the percent of the landscape that is protected (i.e., *PctArea*) can be a sufficient proxy of more complicated alternatives when measuring percent changes in connectivity for area-based conservation targets. If a more complex structural metric is desired, we recommend the Integral Index of Connectivity (*IIC*). We also suggest avoiding metrics that exhibit both positive and negative directional changes in response to an expanding PA network as they may cause confusion in reporting and have adverse consequences for conservation. These metrics include *Prox*, *Compart*, *ClustCoeff*, *Degree*, *Cohesion*, *Gyrate*, *BC*, *BA*, and *AWGyrate*.

5. Conclusion

Findings from this study suggest that simple metrics such as the percentage of area that is protected (i.e., *PctArea*) can be a viable proxy for more structurally complex metrics. Simpler metrics such as *PctArea* are preferred as they are easier to interpret and have higher potential to promote communication with a wider audience (i.e., non-technical) at lower computation cost. While *PctArea* is not a direct measure of the absolute size of the protected areas, its substitutability for more complex metrics nonetheless indicates that area is a key determinant of connectivity. This conclusion is supported by the Pearson's correlation and PCA results. Metric responses to PA network changes were largely consistent across the three study regions. However, in some instances, the tested metrics were observed to be sensitive to differences in the composition and configuration of the PA network.

The findings of this study offer several directions for future research into connectivity and area-based conservation. First, future studies should advance the analysis of incremental PA network change and its relationship with connectivity monitoring. It is common to observe gradual changes in PA networks as areas are added slowly over time. Monitoring PA network changes at this finer temporal scale will be key to developing techniques and advice that can be used in conservation planning and management. Second, in this study, PAs were treated as homogenous within their respective study areas. In reality, PAs vary along numerous dimensions. For example, PAs may differ in their habitat quality, level of management, and ecological integrity. Analyzing changes in connectivity using metrics that can account for these characteristics, as well as PA size and relative position, will be important for measuring connectivity to preserve biodiversity and meet global conservation targets. Finally, as connectivity is scale-dependent and metric performance could be scale-sensitive, we recommend addressing the scale of analysis explicitly in connectivity research and further investigation in metric performance across different scales.

CRediT authorship contribution statement

Wenxin Yang: Conceptualization, Methodology, Software, Validation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Peter Kedron:** Conceptualization, Methodology, Validation, Writing – original draft, Writing – review & editing, Visualization, Supervision. **Amy E. Frazier:** Conceptualization, Methodology, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data are publicly available through the World Database on Protected Areas (WDPA) and the Protected Area Database of the US (PAD-US). A link to the code is provided in the manuscript

Acknowledgements

This research was funded by grants to A.E.F. from the U.S. National Science Foundation (Award #2225079 and #2401273). All processing scripts are available through a public GitHub repository github.com/wxyang007/CompareConnectivityMetric. The authors thank the editor and three anonymous reviewers for their helpful comments, which improved the mansucript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.111387.

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