



Evaluating trade-offs between species targets and average coverage in spatial conservation planning

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ABSTRACT

With global conservation coverage rising toward 30 % and beyond, designing reserve networks that maximize biodiversity benefits while balancing competing objectives remains a pressing challenge. Spatial conservation prioritization methods are essential tools in this effort, yet different approaches can lead to markedly different outcomes. Among these, target-based minimum set coverage planning (MSC) and balanced priority ranking (BPR) represent two fundamentally distinct strategies: MSC focuses on meeting explicit conservation targets, while BPR seeks to achieve a cost-effective solution that maximizes coverage for all features. Despite their widespread use, little is known about how these methods compare in efficiency or differ when applied to the same datasets with varying target strategies. Here, we systematically compared conservation coverage achieved by the two methodologies with equal area allocation using five open datasets and four target-setting scenarios. We found that BPR resulted consistently in higher mean feature coverage per area protected compared to MSC across all datasets. BPR average coverage was nearly twice as high when considering all datasets together, although coverage was heterogeneous and showed no clear minimum threshold. In contrast, MSC guaranteed that specified target levels were met with certainty, but this came at the cost of reduced mean coverage. The magnitude of these differences highlights a major trade-off between targets and mean coverage, emphasizing the importance of disclosing conservation performance rather than solely reporting the proportions of features meeting targets or similar metrics. This can lead to more informed decision-making and improved performance assessments, with significant policy relevance for global conservation planning.

1. Introduction

Effective reserve network design guided by spatial conservation planning plays a crucial role in biodiversity conservation (Watson et al., 2014). With many countries worldwide committing to the Global Biodiversity Framework's target of protecting 30 % of terrestrial, inland water, and of coastal and marine areas by 2030, spatial planning is both highly relevant and urgently needed (CBD, 2022). Within the broad framework of systematic conservation planning, there is usually a step where spatial prioritization (a.k.a. reserve selection, reserve network design, spatial optimization) is applied to biodiversity distribution data to identify the best candidates for reserve network expansion (Margules and Pressey, 2000; Sarkar et al., 2006; Kukkala and Moilanen, 2013).

Over the past few decades, various spatial prioritization approaches have been developed, yet systematic comparisons of these methods still lack clear and conclusive insights into their conservation performance.

The first widely known reserve selection method, known as target-based minimum set coverage planning (hereafter MSC), was developed in the 1990's (Csuti et al., 1997; Pressey et al., 1997). This method originates from applied mathematics in facility location science, and its structural analogues have been applied to various topics, including conservation science (Church et al., 1996). The core principle of MSC is to establish minimum needs (i.e., conservation targets) for services or commodities (here, biodiversity) with the objective of achieving these targets with minimum cost (or area). MSC methods are well known from the software MARXAN, which applies stochastic optimization to solve

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MSC problems (Ball et al., 2009), and more recently from the R package *prioritizr*, which uses exact optimization via Integer Linear Programming (Hanson et al., 2023).

Another commonly used methodology for spatial planning applications is balanced priority ranking (hereafter BPR), known from software such as Zonation (Moilanen et al., 2005; Moilanen et al., 2022). BPR seeks to achieve a cost-effective solution that maximizes coverage for all features (i.e., biodiversity elements such as species or habitats) for any top ranked fraction of the landscape. No targets need to be specified in BPR and both the spatial ranking and feature-specific performance are an emergent outcome of the underlying ranking process (Moilanen et al., 2022). However, targets can be incorporated in a BPR prioritization (e.g., Moilanen, 2007; Wolff et al., 2023), or explored post hoc based on the resulting solution.

These two approaches differ fundamentally in both optimization logic and expected conservation outcomes (Lehtomäki and Moilanen, 2013; Yao et al., 2023). MSC asks: how can we meet predefined representation targets most efficiently? It often aims to determine the cheapest set of planning units, either in area or in costs, for implementing management actions that optimize the achievement of minimum conservation goals. In contrast, BPR aligns with the maximal-benefit problem in systematic conservation planning, asking: how much biodiversity or benefit can we retain (maximize) while minimizing costs, such as area? This difference in optimization logic between the two approaches is reflected in the way benefits are calculated. In a target-constrained problem, for instance, benefit can be described with a step-function (Arponen et al., 2005), meaning areas that do not meet all conservation targets provide no benefit, while those that meet all targets offer maximum benefit. Once a target for a particular conservation feature is achieved, conserving additional areas of that feature yields no further benefit in a MSC optimization. The conservation significance of either meeting all targets or gaining higher average coverage of features will be dependent on case-specific objectives. Despite these fundamental differences, insufficient consideration is often given to whether a BPR or MSC approach is more appropriate before conservation targets are set (Lehtomäki and Moilanen, 2013), potentially constraining the relevance and effectiveness of the resulting prioritization. This is important because MSC and BPR are not only very different in their theoretical and methodological foundations, but also have potentially very different performance characteristics in terms of conservation coverage achieved.

The conservation performance of highly constrained conservation problems may decline because numerous constraints can significantly limit the search space (Laitila and Moilanen, 2012). Here, this statement applies to MSC in the sense that performance can be interpreted as some measure of overall conservation coverage and the targets serve as the (many) constraints applied to the problem. This suggests a potential trade-off between conservation targets and species average coverage. The questions of relevance are: Given that MSC is designed to meet predefined targets, what are the implications of this constraint for conservation performance? How do the results differ between MSC and BPR when applied to the same datasets? Is the difference large enough to matter for conservation policy?

Although analyses evaluating the performance of conservation approaches have been conducted in the past (e.g., Delavennne et al., 2012; Schuster et al., 2020), there remains a limited number of studies comparing conservation planning tools and their outcomes, particularly regarding how variations in target-setting affect conservation coverage. Moreover, it is important to highlight that target-based planning is widely used in conservation, often without sufficient consideration of how targets are set (see Carwardine et al., 2009), such as the common practice of applying the same target (e.g., 30 %) to all features. This oversight can lead to suboptimal outcomes (Laitila and Moilanen, 2012), underscoring the importance of evaluating the trade-offs between meeting conservation targets and achieving higher species average coverage. Gaining such insights is crucial for more effective and transparent decision-making, carrying significant policy implications for

global conservation planning efforts.

Here we systematically compared the conservation performance of MSC and BPR approaches by measuring the conservation coverage each method achieves when constrained to equivalent area allocations. We conducted this comparison across five diverse real-world datasets, differing in resolution, scale, and number of features, chosen to represent a range of scenarios from national to global scales. We also assessed the relationship between conservation coverage and species' range size to understand how these methods perform across species with varying distribution sizes.

2. Methods

2.1. Datasets

We used five previously published and openly available real-world datasets differing in number and size of planning units (ranging from ~75,000 to nearly 1 million units, with spatial resolutions from 1 km to 50 km), number of features (67 to 5608), and spatial scale (from regional to global), selected to represent a wide range of conservation planning scenarios (see Table 1 and Supplementary Material 1 for more details). These datasets consist of species distribution models (SDMs), except the global terrestrial mammals dataset, which contains binary maps derived from IUCN range maps. SDMs represent habitat suitability values across geographic space, whereas the binary maps depict inferred species ranges. We acquired global species range data for all extant terrestrial mammals from the IUCN Red List database (v.2019–2, IUCN, 2019). The other datasets include the global distribution of deep-water corals (Gouvêa et al., 2024), boreal-breeding birds (Stralberg, 2012), butterflies from Borneo (Scriven et al., 2020), and European tree species (Mauri et al., 2022).

2.2. Implementation of MSC and BPR

We employed a simple systematic approach to compare the outcomes of MSC with BPR:

- Establish basic targets for MSC planning. To facilitate comparison, we employed a 10 % flat target, a 20 % flat target, and a 30 % flat target, for all features. Flat target means that all features are assigned the same target of 10 %, 20 %, or 30 % of their distribution size, respectively.
- Solve the MSC problem for each target using the minimum set objective function in the *prioritizr* R package (see Software section).
- Implement BPR by running a default Zonation 5 prioritization on the same data, with all species weights set to 1.0 and no other constraints applied.
- Clip the BPR solution to the top fraction of the landscape corresponding to the spatial area of each MSC solution.

Table 1
Detailed information on the open access datasets used in this study.

Dataset	Planning units	Number of features	Resolution (in meters)	Scale
European trees	130,210	67	10,000	Continental
Butterflies of Borneo	74,784	77	1000	Regional
Terrestrial mammals	68,542	5608	50,000	Global
Boreal-breeding birds	440,204	96	4000	Regional
Deep-water corals	986,664	586	20,000	Global

- Generate conservation coverage histograms to compare each MSC solution with the corresponding clipped BPR solution representing the same spatial area for each target scenario.

The fraction of each feature's full distribution included in the spatial solution is considered its conservation coverage. These conservation coverages can be evaluated with histograms, assessing both the mean coverage across features and the performance in the tails of the histogram. For example, target-based MSC planning guarantees that no feature has coverage lower than the target used, which eliminates the possibility of undesirably poor performance in the lower tail. Effectively, we used these histograms to compare the coverage of feature distributions achieved through BPR with that of target-based MSC planning when using the same amount of area available.

In addition to the three flat targets, we tested an alternative target-setting strategy that scales the targets based on the species' range size, using a log-linear approach (Rodrigues et al., 2004). To ensure replicability across datasets, a 95 % target was used for the species with the smallest distribution in the dataset going down to 20 % for the species with the widest range. Interpolation on a log-linear scale was employed between these two extremes. We explored alternative target-setting thresholds (e.g., 100 % for species with the smallest ranges and 10 % for the largest; or using quantiles, with 100 % for the 10 % quantile of species with the smallest ranges and 10 % for the 90 % quantile of species with the largest). However, these approaches led to impractical solutions, with the MSC selecting all planning units in the study area for some datasets, which made comparisons with BPR unfeasible. Therefore, we proceeded with the 95 % and 20 % thresholds as our main log-linear target-setting strategy.

2.3. Software used

We used the R package *prioritizr* (Hanson et al., 2023) with the Gurobi optimizer v.11.0.1 (Gurobi Optimization, 2021) for the target-based MSC approach. Use of linear optimization has the benefit of generating globally optimal solutions for the MSC problem (Schuster et al., 2020). *Prioritizr* is increasingly used in spatial conservation planning for a range of applications, including the identification of global conservation priorities (Jung et al., 2021), land-use zoning (Law et al., 2021), and designing climate-smart spatial plans (Buenafe et al., 2023).

Zonation 5 v.2.0.2 software was used for BPR (Moilanen et al., 2022). It produces a spatial priority ranking through the landscape, accounting for local occurrence levels and balance (complementarity) between features. Different from MSC planning, both the spatial ranking and occurrence levels of features are an emergent outcome of the balancing and aggregation methods used, and no a-priori setting of targets is required.

In *prioritizr*, we used the `add_min_set_objective()` function to set the objective of the conservation planning problem. To set the targets, we used `add_relative_targets()` and `add_loglinear_targets()` functions. We used the `eval_feature_representation_summary()` function to calculate the proportion of each feature secured within the solution (i.e., the coverage). In Zonation, this is calculated automatically as one of the main outputs. For Zonation, we used the default CAZ2 as the marginal loss rule, which displays a good balance between average coverage and coverage for features that are difficult or expensive to cover (Moilanen et al., 2022).

2.4. Further comparisons

To gain a better picture of the differences between the two approaches, we plotted the coverage of feature distributions in relation to the size of species' ranges. We calculated the Pearson product-moment correlation coefficients to quantify the strength and direction of the relationship between these variables. Range size was calculated as the sum of the feature data across the raster cells. Due to a higher degree of

overplotting, we used the `stat_binhex()` function in the R *ggplot* package to divide the plot plane into regular hexagons and map the density of the points to fill the color of the hexagons.

3. Results

We evaluated the performance of two conservation planning approaches by applying MSC and BPR to five real-world datasets. We found that BPR consistently resulted in higher mean coverage of feature distributions compared to MSC planning with equivalent area allocation, reaching much greater levels in some cases (Fig. 1). This result holds true for all datasets and all targets evaluated here (Table 2 and Supplementary Figs. 2.1–2.2). Applying a non-parametric Wilcoxon test, we found that the differences were statistically significant (Fig. 2). Across all data sets and target levels, the mean coverage of BPR (0.71 ± 0.31 , mean $\pm$ SD) was nearly twice that achieved by the target-based approach (0.40 ± 0.25). The smallest difference was found for the butterflies from Borneo dataset (e.g., target 10 %: BPR: 0.13 ± 0.04 and MSC: 0.11 ± 0.01), whereas the largest difference was observed for the global terrestrial mammals dataset (e.g., target 30 %: BPR: 0.80 ± 0.26 and MSC: 0.40 ± 0.16) (Table 2). No target failure was observed for the MSC approach, meaning that in all MSC solutions, all features met their set targets.

When examining how well species distributions are covered relative to species range size, we found a stronger negative trend for the balanced priority ranking compared to MSC (Fig. 3), supported by higher correlation values. BPR correlations ranged approximately from -0.28 to -0.40 , whereas MSC correlations were weaker, ranging roughly from -0.12 to -0.21 . This difference in the relationship was especially clear for species with small distributions, with BPR tending to provide higher coverage for these species compared to MSC. Beyond these coverage differences, MSC and BPR also differ markedly in their spatial allocation of priorities, selecting distinct sets of planning units (Supplementary Figs. 3.1–3.4). These spatial differences are exemplified by the butterflies from Borneo dataset (Fig. 4).

4. Discussion

We found that BPR consistently leads to higher species average coverage compared with MSC with equivalent area allocation (Fig. 1 and Fig. 2). The observed difference aligns with theoretical expectation (Laitila and Moilanen, 2012), but the size of the difference has not been previously quantified. With the datasets and target levels tested, BPR achieved up to nearly twice the mean conservation coverage of MSC (Fig. 2). The magnitude of this difference shows that there can be a major trade-off between targets and mean coverage, highlighting the conceptual and policy questions of which type of solution is preferable in any specific prioritization study.

According to our results, MSC guaranteed that specified target levels were achieved with certainty, which comes with the price of reduced mean coverage compared to BPR. However, this guarantee technically holds only when using exact optimization techniques such as Integer Linear Programming (ILP). When heuristic methods are used, whether in *prioritizr* or in any other conservation planning tools, there is a risk that not all targets will be achieved. On the other hand, BPR can have high mean coverage, but representation across species is heterogeneous, and the minimum coverage can be lower than that achieved by MSC using equal area allocation (Fig. 1). The size of the difference depends on both the dataset and target levels, with largest differences in mean coverage found for the global datasets (Fig. 1 and Supplementary Figs. 2.1–2.2). Heuristically, this difference arises from the ability of BPR to opportunistically give up coverage for features that are hard or expensive to cover, effectively using the resource to increase coverage for many features in a cost-efficient manner (Moilanen et al., 2022). We have found that conservation coverage histograms are a convenient method for assessing these differences in the aggregate outcome of spatial

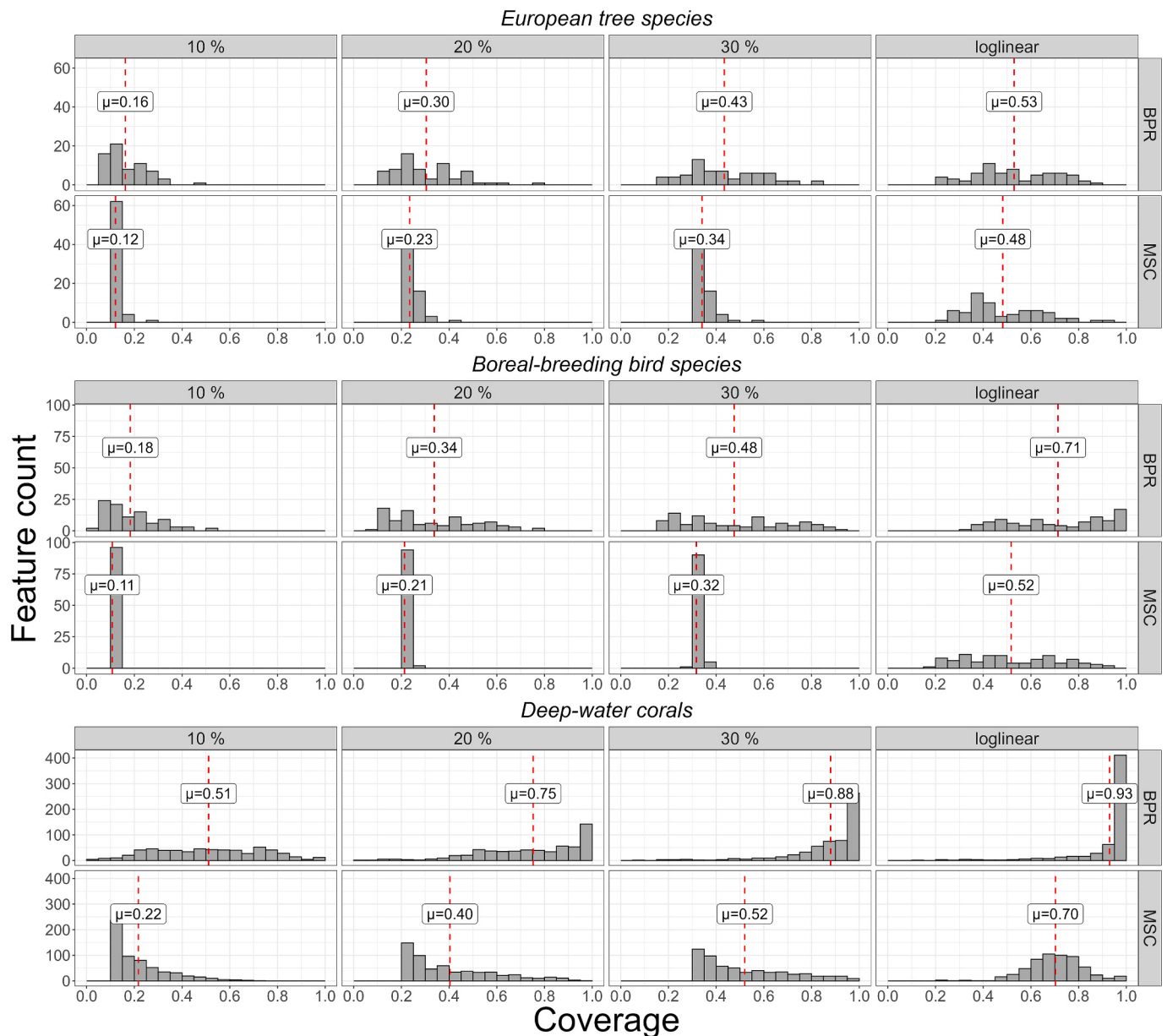


Fig. 1. Comparison of coverage of feature distributions between balanced priority ranking (BPR) and target-based minimum set coverage planning (MSC) at 10 %, 20 %, 30 %, and log-linear targets, for three example datasets: European tree species, Boreal-breeding birds, and deep-water corals. The red dashed line indicates the mean conservation coverage across features (μ). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

prioritization at any given resource level. Given the differences observed in this study, disclosure of performance rather than solely reporting the proportions of features meeting targets or similar metrics becomes crucial, as the aggregate outcome can be an important component influencing conservation resource allocation and action, with potential implications for policy relevant decisions.

Major differences between the two approaches become apparent when considering species range against conservation coverage. The MSC approach effectively ensures that all species meet their conservation targets, reflecting its strength in explicit achieving minimum goals. However, it does not prioritize species beyond these minimums and tends to perform poorly for species with smaller ranges. In contrast, BPR generally provides higher coverage for narrow-range species but results in heterogeneous representation, with no clear minimum coverage threshold guaranteed. This outcome reinforces the trade-off between maximizing average coverage and ensuring minimum protection levels

(Fig. 3). Using the log-linear approach, most species no longer clustered at minimal coverage levels (Fig. 3), reducing these differences, but at the cost of selecting a greater proportion of planning units (area) to achieve the targets (see Fig. 4 and Supplementary Figs. 3.1–3.4). Such area requirements can become exceptionally large, undermining the efficiency of MSC when coupled with a log-linear target approach.

Our findings can also offer practical guidance for choosing between MSC and BPR in conservation planning. MSC could be well suited, for instance, in cases where specific minimum representation targets must be met, such as legal frameworks requiring documented minimum habitat retention (e.g., Soares-Filho et al., 2014; Gairin and Andréfouët, 2020), because it tends to be more cost-efficient at precisely achieving these targets. Such requirements form the basis for accountability and monitoring frameworks that require clear evidence of target fulfillment, ensuring legal and political compliance. However, BPR can also be applied to achieve these targets by selecting priority areas that meet

Table 2

Feature coverage (mean $\pm$ SD) under target-based minimum set coverage planning (MSC) and balanced priority ranking (BPR) across five datasets and four different target-setting scenarios.

Dataset	Target	BPR (mean $\pm$ SD)	MSC (mean $\pm$ SD)
Boreal Breeding Birds	10 %	0.18 $\pm$ 0.11	0.11 $\pm$ 0.01
	20 %	0.34 $\pm$ 0.18	0.21 $\pm$ 0.01
	30 %	0.48 $\pm$ 0.22	0.32 $\pm$ 0.02
	loglinear	0.71 $\pm$ 0.21	0.52 $\pm$ 0.20
Butterflies Borneo	10 %	0.14 $\pm$ 0.05	0.11 $\pm$ 0.01
	20 %	0.27 $\pm$ 0.07	0.22 $\pm$ 0.02
	30 %	0.38 $\pm$ 0.08	0.33 $\pm$ 0.03
	loglinear	0.90 $\pm$ 0.03	0.86 $\pm$ 0.03
Deepwater Corals	10 %	0.51 $\pm$ 0.22	0.22 $\pm$ 0.12
	20 %	0.75 $\pm$ 0.21	0.40 $\pm$ 0.19
	30 %	0.88 $\pm$ 0.16	0.52 $\pm$ 0.19
	loglinear	0.93 $\pm$ 0.14	0.70 $\pm$ 0.12
Eu Trees4f	10 %	0.16 $\pm$ 0.08	0.12 $\pm$ 0.03
	20 %	0.30 $\pm$ 0.13	0.23 $\pm$ 0.04
	30 %	0.43 $\pm$ 0.16	0.34 $\pm$ 0.05
	loglinear	0.53 $\pm$ 0.17	0.48 $\pm$ 0.16
Global Terrestrial Mammals	10 %	0.50 $\pm$ 0.34	0.20 $\pm$ 0.18
	20 %	0.68 $\pm$ 0.31	0.30 $\pm$ 0.17
	30 %	0.80 $\pm$ 0.26	0.40 $\pm$ 0.16
	loglinear	0.90 $\pm$ 0.19	0.70 $\pm$ 0.17

minimum requirements while simultaneously maximizing biodiversity representation. In addition, BPR may be more appropriate for flexible or incremental planning, such as opportunistic land acquisition, ecological impact avoidance, or prioritizing under climate uncertainty where species distributions may shift (Lehtomäki and Moilanen, 2013). This flexibility can enhance conservation effectiveness when rigid targets are difficult to meet, when efforts must respond dynamically to changing ecological conditions, or when insufficient information prevents the translation of representation targets into extinction risk (Moilanen, 2007; Carwardine et al., 2009).

This last point is notable from the perspective that setting ecologically meaningful and accurate targets is a highly non-trivial task, and even small changes in the targets between features can significantly alter the final solution (Carwardine et al., 2009; Levin et al., 2015). Target setting remains highly challenging because it requires quantifying the “minimum area” necessary for a species to survive in a manner that is both consistent and effective across all species in the planning problem (Carwardine et al., 2009). Unfortunately, there is often insufficient data to make accurate estimates for most species, resulting in targets that are frequently set arbitrarily. Nevertheless, the compelling results obtained

here pave the way for exploring other important questions in future studies. Conceptual differences between software, operational aspects of software implementations, the impact of data dimensionality on optimization convergence, and other objective functions could be further investigated. The example curated dataset and code provided with this study could serve as valuable resources for exploring these aspects further.

The main aim of the present study was not to draw overarching conclusions about the suitability of a single approach for all conservation planning contexts. Both approaches evaluated here have yielded exceptional outcomes, bringing significant benefits to both nature and people (Sinclair et al., 2018). Conservation planners should choose the software or problem definition that best aligns with their project's specific objectives and the unique functionalities offered by different tools. Our focus, instead, was to provide clear and robust results concerning biodiversity outcomes, with particular emphasis on comparing different approaches in terms of conservation coverage, representation, and their ability to effectively address ecological trade-offs. We emphasize that relying on a single framework in isolation may limit its potential benefits, as no one framework can address the full range of conservation planning and decision-making processes and challenges (Schwartz et al., 2018). Notably, previous work has successfully integrated both approaches by combining contrasting planning goals within a multi-scenario prioritization framework that accounts for policy considerations, enhancing the practical application of conservation plans in complex real-world contexts (Yao et al., 2023).

To conclude, there is a clear tradeoff between mean conservation coverage and the use of feature-specific targets. The relevance of this observation is related to the question: how confident are you about your targets (see Carwardine et al., 2009; Levin et al., 2015; Plumptre et al., 2024)? Irrespective of the reply to this question, investigating these differences in any case study is important. It can reveal critical insights into the trade-offs involved, guide more informed decision-making, enhance the robustness of the optimization strategy, and ultimately influence policy decisions.

CRediT authorship contribution statement

Thiago Cavalcante: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Heini Kujala:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Elina A. Virtanen:** Writing – review & editing, Methodology. **Louise O'Connor:** Writing – review & editing, Methodology. **Pauli Lehtinen:** Writing – review &

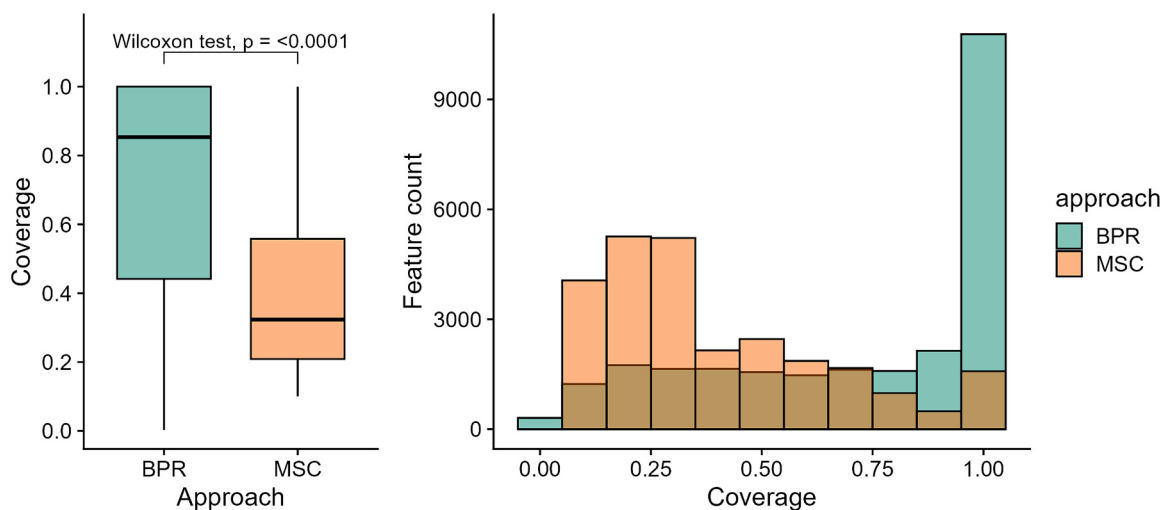


Fig. 2. Differences in coverage of feature distributions between balanced priority ranking (BPR) and target-based minimum set coverage planning (MSC) using merged data from all five datasets. The histograms show the frequency distribution, providing a detailed view of the data spread and concentration.

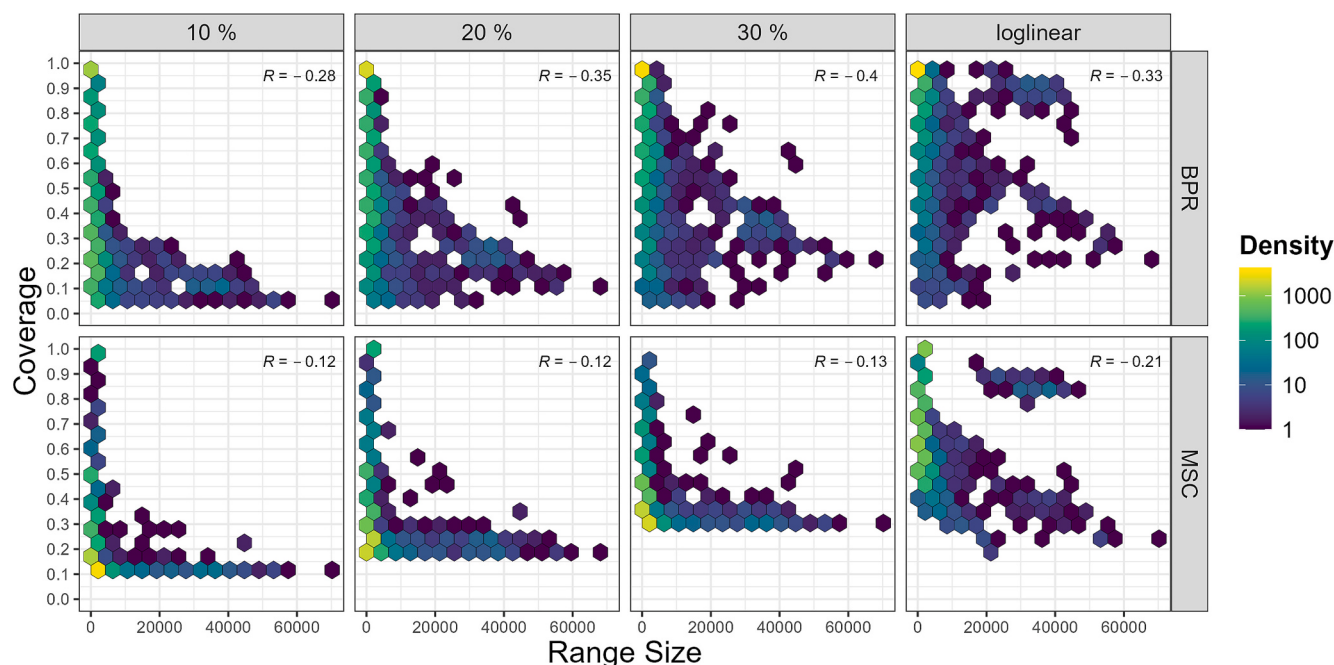


Fig. 3. Relationship between conservation coverage and species range size at 10 %, 20 %, 30 %, and log-linear targets for balanced priority ranking (BPR) and target-based minimum set coverage planning (MSC), using merged data from all five datasets. The inset values represent the Pearson product-moment correlation coefficients (R).

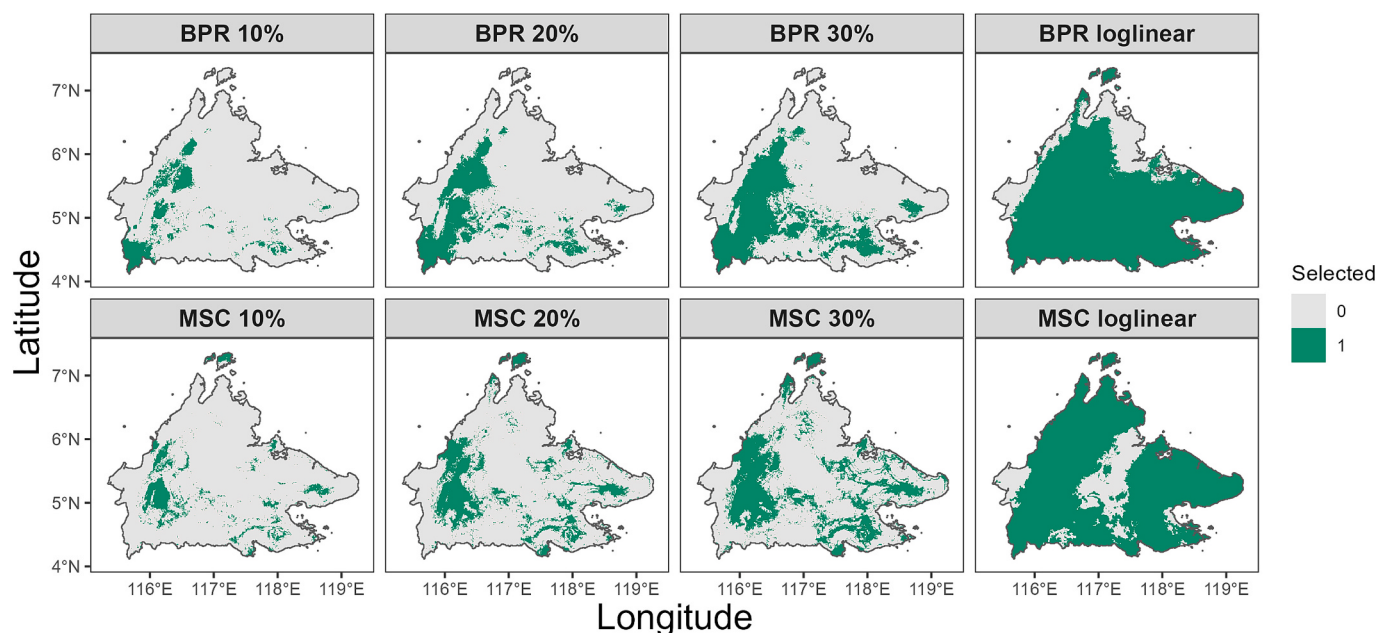


Fig. 4. Differences in the spatial configuration of prioritization solutions produced by balanced priority ranking (BPR) and target-based minimum set coverage planning (MSC) at 10 %, 20 %, 30 %, and log-linear targets using butterflies from Borneo data as example. The legend indicates areas selected under each approach and target setting.

editing, Software. **Atte Moilanen:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Conceptualization.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111368>.

Data availability

All data used in this manuscript are accessible from the original source or linked in the manuscript. A curated dataset and example code supporting the analyses are publicly available at <https://github.com/thiago-cav/conservation-planning-tradeoffs-paper>.

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