

Original Articles

Site selection algorithms for optimal ecological monitoring design

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ABSTRACT

Comprehensive monitoring of biodiversity to direct conservation action is foundational to addressing the ongoing biodiversity crisis. As integrative monitoring programs increasingly come online in response to multilateral biodiversity agreements, establishing best practices for optimal design is critical. Appropriately selecting monitoring locations is fundamental for producing robust biodiversity data. Despite extensive development of algorithms to systematically select sites, practical discussions of which algorithm is optimal for different monitoring settings is largely absent from the literature. Here, we benchmark the performance of four common selection algorithms, outline the characteristics of the suite of algorithms suitable for ecological monitoring design, and offer recommendations for their best use under different constraints on network design. While all algorithms outperformed simple random samples, performance differences were negligible between algorithms. We recommend instead that practitioners choose algorithms based on feature availability, which varies greatly between algorithms.

Monitoring changes in biodiversity through time and across space is fundamental for identifying areas of high conservation value amidst the ongoing sixth mass extinction. Historically, biodiversity data has been dominated by heterogeneous non-probability samples, often collected for snapshots of time using bespoke protocols with low replication (Boyd et al., 2023). Synthesis of this data for broad-scale assessment of biodiversity suffers from low power, severe data biases (Chapman et al., 2024), and an inability to detect existing trends (Boënnec et al., 2024; Johnson et al., 2024; White, 2019). With this context, establishment of standardized monitoring protocols across the globe has been a major focus of multilateral biodiversity agreements (Gonzalez and Londoño, 2022; Griffith et al., 2024).

Monitoring networks that produce robust data for statistical inference are designed under a pre-established statistical framework (Benedetti et al., 2017; Dumelle et al., 2022; Williams and Brown, 2019). In the context of biodiversity monitoring, a network, or biodiversity observation network, refers to a system of sites where identical samples are taken following standardized protocols. At its most basic, the network design process involves (i) defining a sample frame, (ii) identifying potential sampling sites, and (iii) applying a site selection algorithm to identify final sample points. Site selection algorithms select sample sites following random sampling principles while accounting for site locations to identify an optimally spatially balanced sample. Many algorithms support additional features, including incorporation of site level characteristics, systematic over-samples, and

stratification to further tailor the network design (Kermorvant et al., 2019; Stevens and Olsen, 2004; Robertson et al., 2024). Regardless of the specifics of each algorithm, sets of sampling points recommended in this way should offer a fair representation of the statistical structure of the data used to select them, and therefore adequate information about the status and trends of biodiversity in the region.

Despite significant recent investment in tools for designing and implementing monitoring programs, discussions around choosing the appropriate site selection algorithm have been largely restricted to theoretical differences between algorithms or benchmarking of performance using a limited set of metrics rather than practical considerations (Benedetti, 2015; Benedetti et al., 2017; Kermorvant et al., 2019). This is despite significant differences in computational performance, available features, and ongoing development of better-performing algorithms. Previous evaluations largely focus on spatial balance alone rather than a network's ability to meet the goals of a monitoring project (e.g. Di Biase et al. (2024); but see Convertino et al. (2015) for an example of ecological performance metrics). In biodiversity monitoring this may include for example how completely the full species richness of the region is sampled, how well the network captures landscape heterogeneity, or the ability of a network to detect trends through time. There is therefore a critical need for review of site selection algorithms, the features they provide, and how they perform for ecologically relevant metrics.

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Table 1
Available features and implementation for spatial sampling design algorithms.

Algorithm	Abbreviation	Stratification	Auxiliary variables	Legacy sites	Master sample	R package
Generalized random tessellation stratified	GRTS	Yes	No	Yes	Yes	spsurvey, Sdraw
Cube sampling	Cube	Yes	Yes	No	No	BalancedSampling, sampling
Local pivotal method	LPM	No	Yes	No	No	BalancedSampling
Spatially correlated Poisson sampling	SCPS	No	Yes	No	No	BalancedSampling
Balanced acceptance sampling	BAS	Yes	No	Yes	Yes	Sdraw, spbal
Halton iterative partitioning	HIP	No	No	No	Yes	Sdraw, spbal
Dynamic assignment sampling	DAS	No	Yes	No	Yes	

Here, we outline the feature and performance considerations for site selection algorithms using the Canadian province of Quebec as a case study. We describe a typical process for designing a monitoring network, outline the characteristics of common and more recently developed site selection algorithms for biodiversity monitoring applications, and simulate that process for common algorithms to evaluate performance for multiple management-relevant goals. Based on this simulation study, we offer some specific guidance regarding the selection and use of site selection algorithms for integrative biodiversity monitoring (Convention on Biological Diversity, 2022).

1. Methods

1.1. Algorithm descriptions

Algorithms vary widely in their approach to balancing samples across space and site characteristics. Below we describe the site selection process for algorithms, their features, and how they might be implemented in the R programming language. We discuss stratification, incorporation of site-level data in the form of auxiliary variables, and inclusion of legacy sites to support iterative network development. We also discuss whether or not the algorithm supports master sampling defined as systematic oversampling to support dynamic sample sizes.

The first four algorithms are the most widely accepted and therefore included in our performance benchmarking simulations (Generalized Random Tessellation Stratified, Cube Sampling, Spatially Correlated Poisson Sampling, Local Pivotal Method), with three additional algorithms that hold promise but were not included in benchmarking (Balanced Acceptance Sampling, Halton Iterative Partitioning, Dynamic Sampling Assignment). Algorithm characteristics are also summarized in Table 1.

Generalized Random Tessellation Stratified (GRTS): This algorithm was developed by the U.S. Environmental Protection Agency for use in the National Environmental Monitoring and Assessment Program (Stevens and Olsen, 2004). It uses a hierarchical sampling approach whereby the study extent is hierarchically subdivided by grids until each cell contains only one sample unit. Cells are then ordered on a line by their hierarchical “address”, the line is split into a number of equally sized units equal to the sample size and a sample point is randomly selected from each unit (Benedetti et al., 2017). Rather than incorporating auxiliary data directly into the site selection process, they can be qualitatively assessed by the user to differentially weight site selection or to define stratification. As this is a more subjective process and not directly comparable to auxiliary inclusion for other algorithms, we did not include GRTS in our auxiliary data simulation scenarios. GRTS is one of two algorithms we discuss that supports legacy site inclusion (Foster et al., 2017). We implemented this algorithm using the `grts` function in the R package `spsurvey`.

Cube Sampling: The cube methods seeks to select a sample that balances across auxiliary variables while maintaining the inclusion probabilities of constituent sites (Chauvet and Tillé, 2006; Tillé, 2011). It conceptualizes each potential site as a vertex of a hypercube in an N -dimensional space, R^N . The vector of inclusion probabilities is a vector inside the unit cube, and an affine subspace (hyperplane) defines the set of possible solutions balancing across auxiliary variables. The algorithm

therefore seeks to find a point on the linear subspace that satisfies the inclusion probabilities. Inclusion of auxiliary data is fundamental to this approach and it can also handle stratification by selecting samples with an exact sample size within stratum while still maintaining balance for the network of sites as a whole (Chauvet, 2009). We implemented this algorithm with the R functions `cube` and `cubeStratified` in the R package `BalancedSampling`.

Spatially Correlated Poisson Sampling (SCPS): This algorithm uses a sampler that visits sites one by one, with visit probability initially given by inclusion probability of sites (Grafström, 2012). Subsequent sites are visited after calculating a penalization based on distance to previously visited sites. Auxiliary variable information can be incorporated alongside spatial distance to target optimal spread across variables (Zhao and Grafström, 2020). Since SCPS is designed to account for differences between site characteristics without stratification we use two different stratification approaches for benchmarking. First, the naive approach which simply treats stratification levels as independent samples, and second, an unequal probability sample which enforces within-strata sample size by setting the total inclusion probability for candidate sites in a strata to the desired sample size for that strata (Benedetti, 2015). In benchmarking results below we present the second implementation alongside other algorithms (referred to simply by SCPS), and discuss the comparison between the two implementations separately. We implemented SCPS using the R function `SCPS` in the R package `BalancedSampling`.

Local Pivotal Method (LPM): This algorithm selects sites based on their euclidean distance in the auxiliary sample space. Sites are selected to maximize the distance between points and therefore coverage of the sample space (Grafström et al., 2012). We implemented LPM using two different algorithms: LPM1, which creates the optimally balanced sample, and LPM2 which selects a sample more efficiently (Benedetti et al., 2017). Algorithms performed almost identically, so we report results for only LPM2 here. LPM follows the same philosophy of SCPS in balancing across characteristics without strata, so we also simulated naive and unequal probability stratification scenarios for LPM1 and LPM2. As with SCPS, we include the unequal probability implementation when comparing to other algorithms, and discuss the comparison between naive and unequal implementations separately. These algorithms were implemented using functions `lpm1` and `lpm2` from the R package `BalancedSampling`.

Balanced Acceptance Sampling (BAS): BAS selects points based on a random-start Halton sequence, which gives a quasi-random number sequence (Robertson et al., 2013). The multi-dimensional study space, which could be for example a two-dimensional space defining latitude and longitude, is scaled and enclosed by a unit box of the same dimensions as the study space. Points are then assigned an element of the Halton sequence based on their location in the multi-dimensional box and selected for the final sample set based on the ordering of the sequence. This algorithm does not allow for the inclusion of auxiliary data beyond the ad hoc modification of inclusion probabilities based on site characteristics however it does support the inclusion of legacy sites.

Halton Iterative Partitioning (HIP): This algorithm builds on the concepts of BAS, but rather than selecting points from the space of the multi-dimensional box it iteratively partitions the box and selects

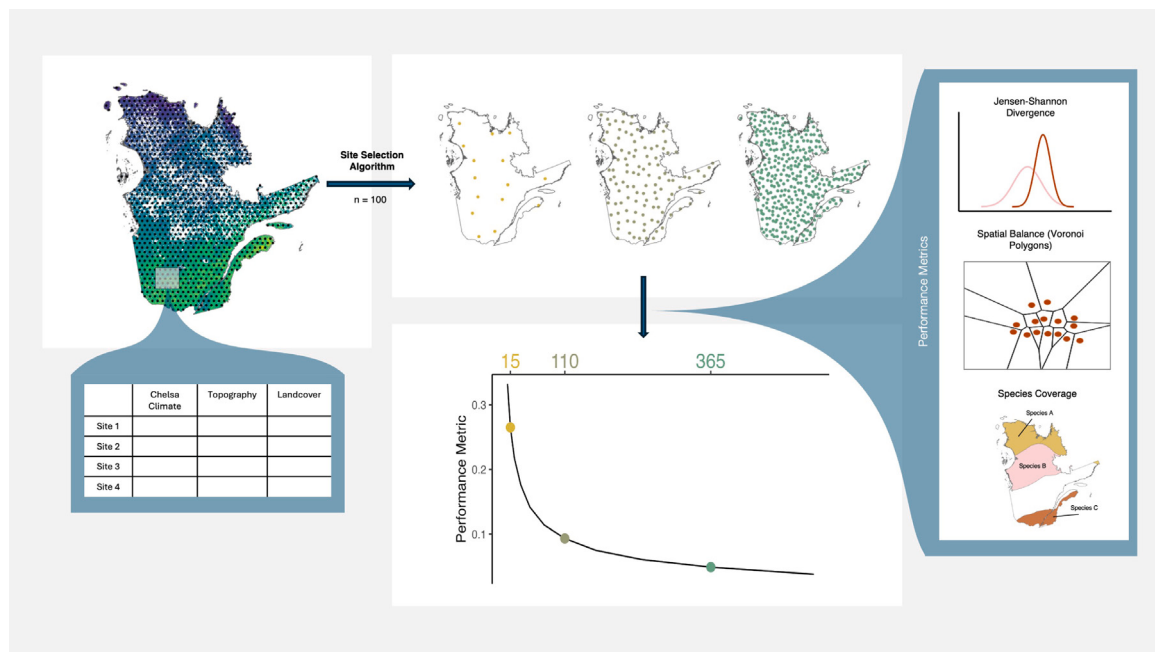


Fig. 1. Conceptual figure depicting the monitoring network design and evaluation process, wherein (1) a set of candidate points are identified, each with their own species and environmental characteristics, (2) designs selecting from the candidate points are generated for each algorithm, scenario, and sample size, (3) those designs are evaluated using the three performance metrics depicted on the right, and (4) performance curves across sample size are then generated for each algorithm and design scenario. Jensen–Shannon divergence compares the complete environmental space to the sampled space, spatial balance determines the distribution of samples across Voronoi polygons, and species coverages identifies the number of species sampled based on their range.

points from the nested boxes based on the Halton sequence ordering (Robertson et al., 2018). It has been recently expanded from its original implementation to facilitate master sampling (Robertson et al., 2022). It does not incorporate stratification or the inclusion of auxiliary variables.

Dynamic Assignment Sampling (DAS): DAS was designed to facilitate the inclusion of auxiliary variables and master sampling in a single algorithm (Robertson et al., 2024). It draws a balanced sample from the auxiliary sample space sequentially as units are iteratively assigned to a candidate set. A candidate set is then chosen as the core set of seed sites before a sufficient number of sites are assigned to reach the desired sample size. DAS has not yet been implemented in open source software at the time of writing.

1.2. Design process

Here we give a general outline for the steps in the simulated network design, with details of data and simulation methods to follow. The design process is depicted graphically in Fig. 1.

Identify Sample Frame: We chose the Canadian province of Quebec as our sample frame of interest as a landscape with a significant latitudinal gradient in environmental variables and biodiversity. It therefore provides a good test of the algorithm's performance across a highly heterogeneous landscape with strong spatial structuring.

Candidate Points: We identified a set of candidate points using a hexagonal sampling algorithm implemented by the R function `st_sample` from the R package `sf`. This algorithm establishes a grid of evenly spaced sample points across the sampling extent while accounting for irregularity in sample extent boundaries. The initial grid had 10000 candidate points evenly spaced across the province of Quebec, with a euclidean distance between points of ~13 km. We excluded points on water or ice as identified by the land cover data described below. The final candidate set had 9992 potential sites. For simulations stratified by ecoregion, we excluded ecoregions with an insignificant area in Quebec, defined by 10 or fewer candidate points in the ecoregion.

Auxiliary Variables: For each potential sample site in the candidate set we assembled a suite of auxiliary variables describing the site characteristics from existing open source environmental data. Data included land cover, climatic variables, and site topography. To account for covariation in variables, we performed whitening on the matrix of auxiliary variables using the function `whiten` from the R package `whitening`. Whitening transforms the sample matrix to a matrix of orthogonal, and therefore independent, variables with unit variance and zero covariance (Kessy et al., 2018).

Identifying Sample Points: For each algorithm of interest we simulated a suite of design scenarios by sampling from the set of candidate points under different conditions. We included a simple random sample as a baseline for performance (Kernmoran et al., 2019) and evaluated the following algorithms: Generalized Random Tessellation Stratified (GRTS), Cube sampling, Spatial Correlated Poisson Sampling (SCPS), and two implementations of the Local Pivotal Method (LPM1, LPM2). For each algorithm we sampled 100 replicates for each sample size ranging from 10 to 545 on an approximate log scale (10, 15, 22, 33, 49, 74, 110, 164, 245, 365, 545). This process was executed for each algorithm for four different sampling scenarios: unstratified (equal probability) and stratified by ecoregion, with and without auxiliary environmental data. For stratified samples, the complete monitoring network sample size was allocated across ecoregion strata proportional to the ecoregion's area in the study extent.

Evaluation of Algorithm Performance: Algorithm performance was evaluated based on three complementary metrics representing different goals for monitoring programs. Spatial balance, or the variance in site inclusion probabilities across space; species coverage, or how comprehensively the network samples existing species on the landscape; and environmental coverage, or how balanced sampling is across combinations of environmental variables. Species and environmental coverage were averaged across simulation replicates and spatial balance was measured as the variance across all simulation metrics. See the Algorithm Evaluation Metrics section below for details on how metrics were calculated.

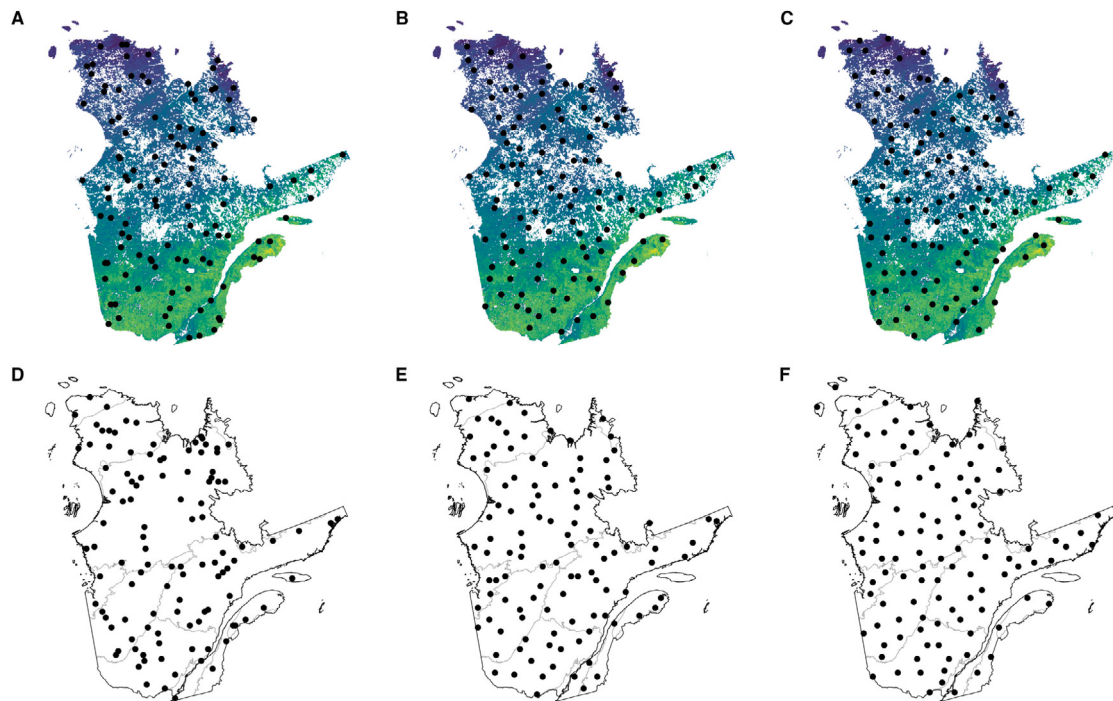


Fig. 2. Example designs for unstratified (A–C) and stratified (D–F) monitoring network designs for Cube (column 1), Local Pivotal Method (column 2), and Spatially Correlated Poisson Sampling (column 3) algorithms, all with a sample size of 110. Unstratified designs are shown with NDVI, stratified designs are shown with ecoregion boundaries.

1.3. Data

Land cover data for candidate point exclusion and auxiliary variables was obtained from the ESA WorldCover dataset for 2020 (Zanaga et al., 2021). Additional auxiliary variables included slope and elevation from the Earthenv topography data (Amatulli et al., 2018), and all 19 CHELSA-BIOCLIM+ variables (Brun et al., 2022). Ecoregions for stratification simulations were taken from the WWF defined ecoregions (Olson et al., 2001). We used IUCN range maps for mammals to evaluate biodiversity coverage of the simulated network and included all mammals whose range intersects with Quebec. While range maps have well discussed inaccuracies and may overestimate species occurrence (Hurlbert and Jetz, 2007), those departures from ecological reality are unlikely to impact algorithms differently, but rather lead to early sampling curve saturation for all algorithms similarly. We therefore feel comfortable using them for species sampling evaluation as the best available dataset of comprehensive mammal occurrence for the region.

1.4. Algorithm evaluation metrics

We evaluated algorithm performance using three metrics that measure complementary goals of biodiversity monitoring networks: spatial balance, species coverage, and environmental coverage. These metrics underpin a network's ability to detect unbiased trends in populations, a common monitoring goal, by measuring how comprehensively spatial, environmental, and species processes are sampled. The power to detect a true trend for a population beyond these factors is a function of sample size and the strength of the trend, a process that is dependent on species biology and outside the scope of this paper (Banner et al., 2019; Wood et al., 2019). Spatial balance is the traditional metric used to assess how a spatial sample is distributed across the sample area, and describes how inclusion probabilities of individual points are distributed across Voronoi polygons. We assessed spatial balance following Benedetti (2015) and Stevens and Olsen (2004) as the variance in total inclusion probability of points contained in each

Voronoi polygon. Lower spatial balance values imply lower variance and therefore fewer unsampled regions with much higher or lower inclusion probabilities of constituent sites, and therefore a better spatial sample.

Fully sampling across the range of environmental conditions in the study area ensures samples span available niche space and capture the relationship between populations and change drivers that may vary by environmental context. We therefore used environmental coverage as an ecological performance metric, measured by calculating the Jensen–Shannon divergence (JSD) for the environmental values represented by a sample network using the function JSD in the R package *philentropy* (Drost, 2018). Jensen–Shannon distance was calculated for each environmental variable, with the JSD for a potential sampling design calculated as the square root of the mean distance of all environmental variables. JSD therefore measures how completely the sample distribution covers the environmental space of the sample landscape. We assessed species coverage using the IUCN range maps to compile species checklists for each sample point and the sample extent as a whole. For ease of interpretation across metrics where higher values indicate worse performance and lower values indicate better performance, coverage was quantified as the percent of species in the landscape not sampled by a given sample monitoring network.

2. Results

Algorithms generally showed very similar performance across metrics, despite having visually different samples (Fig. 2), and showed saturating performance with increasing sample size, particularly for species and environmental coverage (Fig. 3). Across all metrics and simulation scenarios algorithms performed better than the simple random sample. For species and environmental coverage performance differences were negligible, though LPM, and SCPS consistently performed better for all metrics. Cube sampling alone showed marked difference after adding stratification. Surprisingly, including environmental variables did not change algorithm performance significantly for the majority of algorithms, with the exception of cube sampling (Fig. 4).

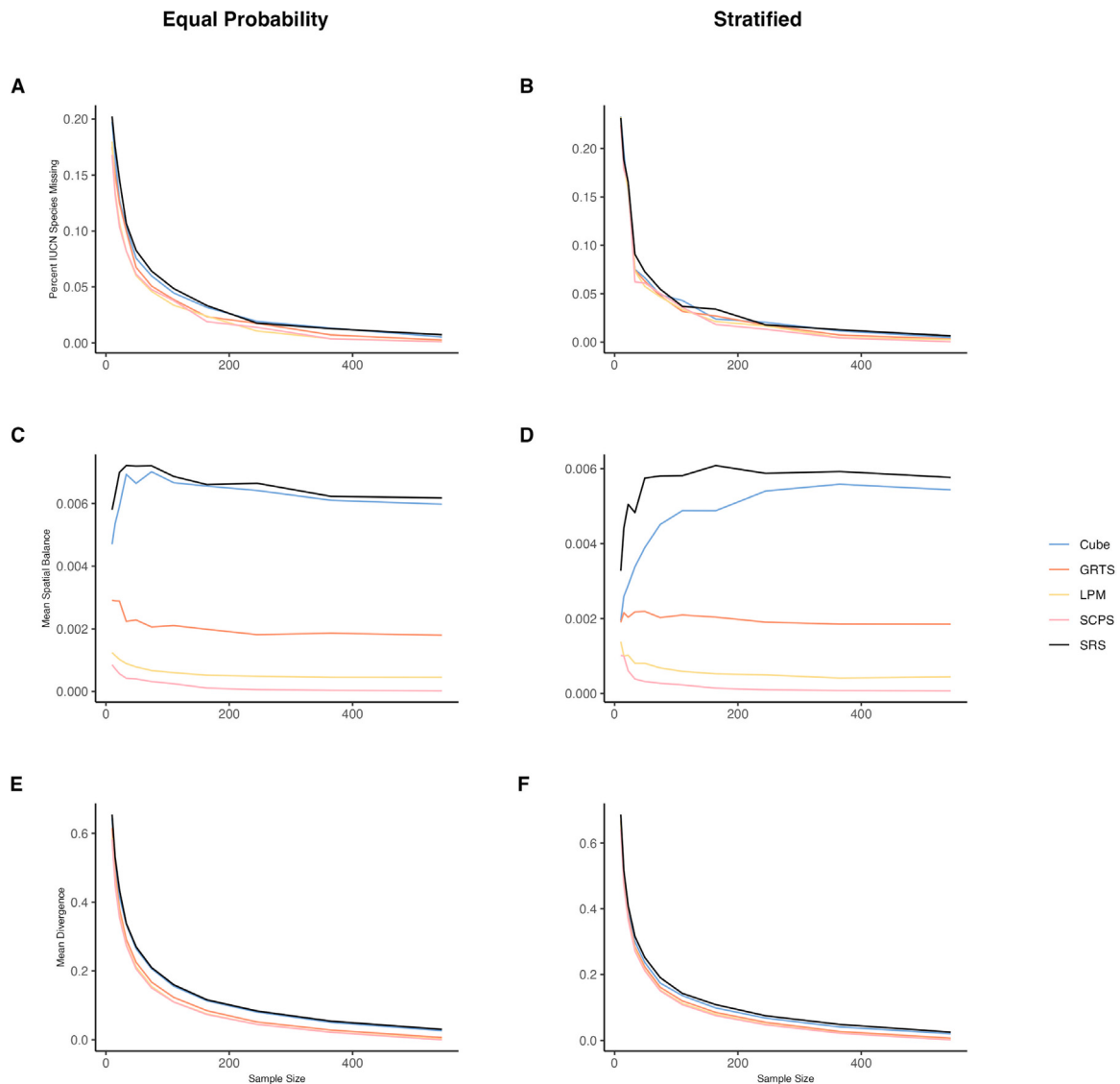


Fig. 3. Three evaluation metrics for each of the algorithms for all of Quebec and stratified by ecoregion. Y axis is scaled between zero and one, with lower values indicating better performance for all metrics.

We found that the naive implementation of LPM and SCPS, where strata were each treated as independent samples, gave significantly worse performance than the unequal probability approach to stratification (Fig. 5). Rather than reaching a saturation point, spatial balance for the naive implementations increased with increasing samples, indicating worse balance with larger sample size. This also manifested in species and environmental coverage, where naive implementations saturated at worse performance than the unequal probability implementations.

3. Discussion

Appropriately selecting sample locations is critical for generating robust inference from biodiversity monitoring data. Despite a variety of existing algorithms for designing a sampling network, and on going development of available features, discussion around the most appropriate algorithm for ecological sampling has been limited. We found the performance differences between most of the best-performing algorithms to be negligible; this was particularly true for species and environmental coverage, and robust across study design. This may simply reflect the fact that ecological processes tend to be correlated to

one another in addition to being spatially auto-correlated (Legendre, 1993). Whereas auto-correlation can be a source of bias by masking actual trends in biodiversity (Diniz-Filho et al., 2003), it can be a net positive for the design of biodiversity monitoring networks by artificially driving algorithms to suggest designs with similar performances. With such similar performance across a broad sample frame with significant gradients in both environment and species variables, biodiversity monitoring performance appears to be limited more by the environmental and biogeographic characteristics of the monitoring region than by the choice of algorithm (we moderate this statement for specific cases further on).

We found that the ecological performance metrics, environmental and species coverage, were even less sensitive to algorithm than the traditional spatial balance metric. Even when spatial balance indicated relatively poor performance (less optimal distribution of sites in space relative to their inclusion probabilities), ecological performance metrics were mostly determined by sample size. Notably, the saturation of performance for ecological performance metrics was similar across algorithms. This, again, reinforces the idea that the “best” designs generated by each algorithm may be equivalent, and that any probabilistic design with sufficient sample size to reach adequate coverage of ecological characteristics is an appropriate design. Although the

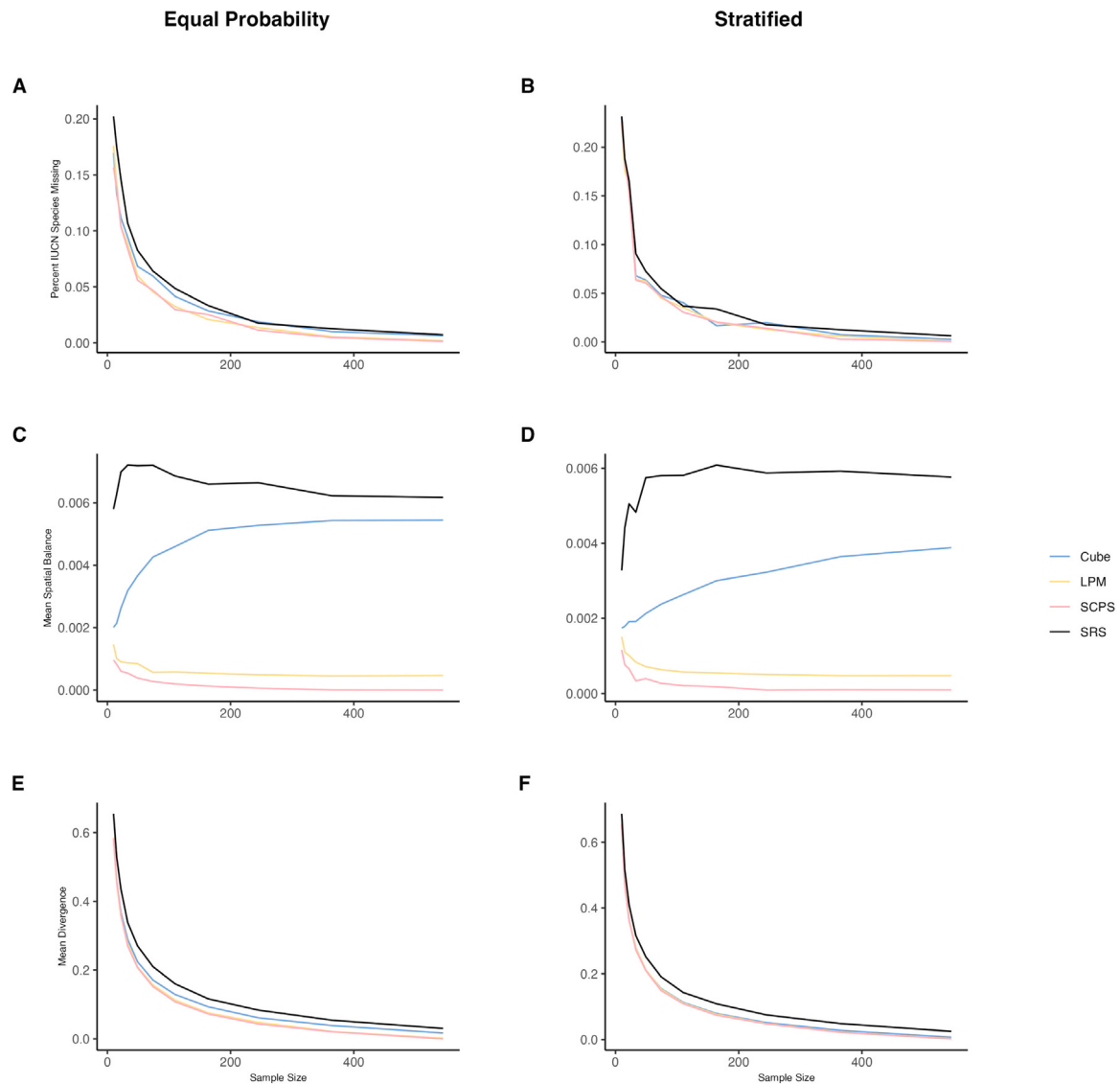


Fig. 4. Three evaluation metrics for each of the algorithms for all of Quebec and stratified by ecoregion, including only algorithms that can take environmental data as auxiliary variables. The Y axis is scaled between zero and one, with lower values indicating better performance for all metrics.

monitoring networks got progressively better with more samples, we observed a clear saturation, suggesting that past this saturation point adding additional sites does not result in more informative monitoring.

Stratification is a common design approach for strategically reducing variance to improve estimator precision (Williams and Brown, 2019), and our results give important clarification on appropriate stratification implementation across algorithms. Stratified samples in non-spatial settings treat strata as fundamentally independent, with samples drawn from each strata without information from other strata. In spatial samples, treating strata independently creates boundary effects as the spatial properties of samples in adjacent strata are not taken into account. This is the phenomenon captured by our naive implementation of LPM and SCPS (Fig. 5), where spatial balance performs worse with increasing sample size as the sample frame becomes more saturated and boundary effects are amplified. Larger samples therefore perform worse at capturing processes with a spatial component. Algorithms that incorporate stratification (GRTS, Cube, BAS; Table 1) iteratively take into account the samples in neighboring strata to spatially optimize across the sample frame. Thus, while LPM and SCPS do not follow stratification principles, the closest equivalent for applications where stratification is necessary is to enforce sample sizes for individual stratum via site inclusion probability, allowing the

algorithm to take into account the entire sampling frame. This approach is demonstrated in our unequal probability implementation.

Our results also support algorithm-specific recommendations for cube sampling, whose performance increased relative to other algorithms when auxiliary data were used. This algorithm is therefore unsuitable when there are no readily available information about non-ecological data at the candidate locations. Although this is a limitation, the wealth of publicly available high-resolution geospatial data means that this limitation is unlikely to ever affect the viability of cube sampling as a site selection algorithm. Beyond those specific stratification and cube sampling use cases, algorithm selection is largely dependent on the features needed by the user and implementation availability (Table 1), even more so since no algorithm was able to generate a monitoring network that saturated with fewer sampled locations.

We benchmarked algorithms for a single case study landscape, defined by its large extent and strong latitudinal gradient in species richness, composition, and environmental features. The performance of some algorithms may respond to changes in the landscape of interest. For example, highly heterogeneous landscapes may be more comprehensively sampled by algorithms that take into account site-level information; this is particularly likely since fine-scale heterogeneity can over-rule the effect of auto-correlation (Tardano and Hovestadt,

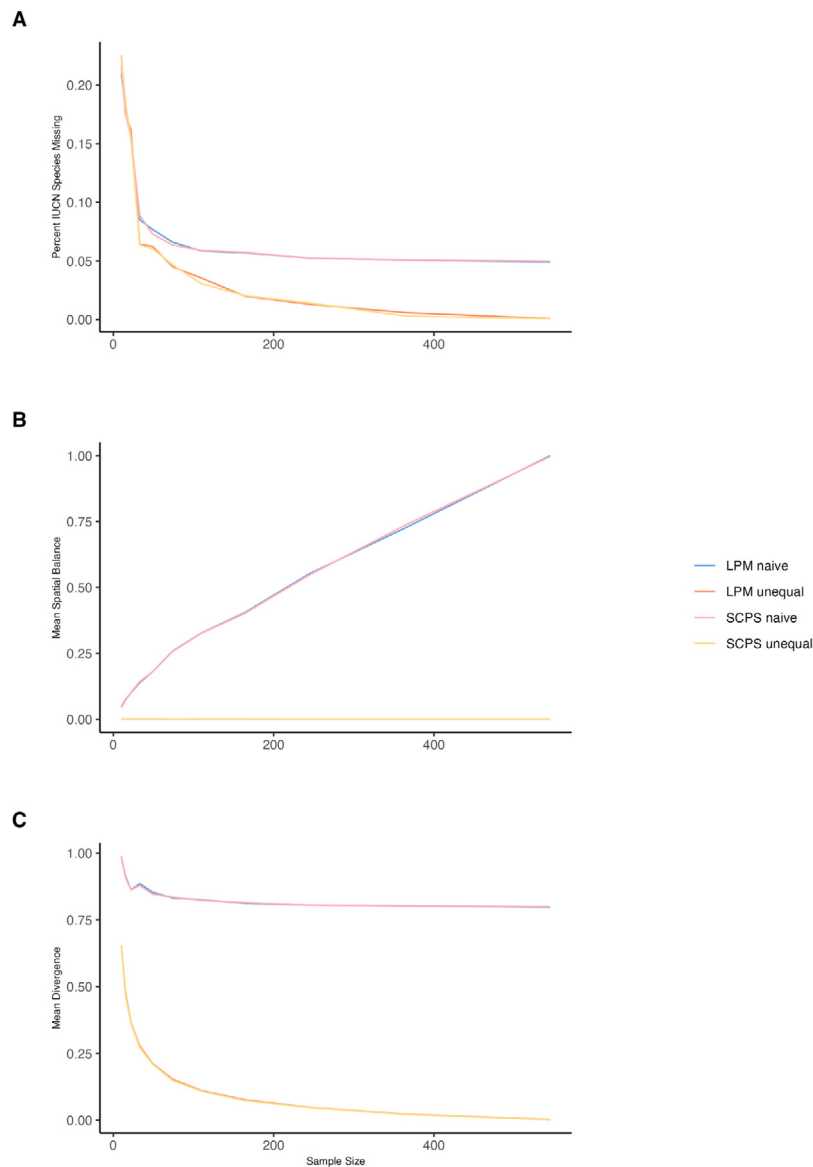


Fig. 5. Three evaluation metrics for naive (stratum treated completely independently) and unequal probability (enforcing strata sample size by modifying inclusion probabilities) implementations of Local Pivotal Method and Spatially Correlated Poisson Sampling algorithms. Unequal implementations are the same show in benchmarking in Figs. 2 and 3.

2023), which can reveal additional differences between algorithms. Similarly, ecosystems in which species distributions are not tightly tracking the environmental gradient may lead to some algorithms achieving better performance; we specifically expect that in these cases, algorithms with good spatial balance may be more apt at capturing ecological variables. As algorithm equivalence may not be guaranteed based on these factors for different regions or data sources, we encourage future researchers to follow the general structure of this study to benchmark algorithms for particular problems. Adopting benchmarking as a necessary step in the design process will be critical for further exploration of algorithm sensitivity to ecological characteristics. It may also be particularly useful in tandem with monitoring network power analyses that assess required sample size to detect phenomena like population trends, where differences in sample location and not just sample size may play a role in network power.

The option to produce a master sample is a key distinguish feature of algorithms with particular relevance to ecological sampling (Robertson et al., 2024). Master sampling creates a systematic oversample (*i.e.* recommends more points for inclusion than required), facilitating an

increase or decrease in the sample size dynamically while maintaining the probabilistic sampling frame (van Dam-Bates et al., 2018). This approach facilitates modifications to the complete set of sampling locations due to common logistical constraints such as site inaccessibility, changing landownership, or budgetary constraints. Of the algorithms we benchmarked only GRTS can create a master sample, however it is increasingly recognized as a critical feature for robust implementation of monitoring designs. This is reflected in recent algorithm development with BAS, HIP, and DAS all supporting master sampling (Table 1).

Comprehensive understanding of available metrics, their characteristics, and performance are critical for the ongoing investment in expanding biodiversity observation networks. Limited differences in algorithm performance indicate that users should give more importance to the features of each algorithm when selecting a subset to benchmark against for a specific region of interest. All the algorithms we benchmarked were able to outperform simple random sampling, reinforcing their necessary use in the monitoring design process to generate robust biodiversity monitoring networks over naive or expert-informed

sampling alternatives. Although all but one of these algorithms had available implementations, they used very different interfaces and programming conventions. The development of a unified interface for sampling is a natural next step in facilitating sampling algorithm uptake for addressing multilateral biodiversity monitoring agreements.

CRediT authorship contribution statement

Kari E. Norman: Writing – original draft, Formal analysis, Data curation, Conceptualization. **Timothée Poisot:** Writing – original draft, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: 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.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.ecolind.2025.114104>.

Data availability

Code is archived at [10.5281/zenodo.14853263](https://zenodo.org/record/14853263) and raw and interim data products are archived at [10.5281/zenodo.14853272](https://zenodo.org/record/14853272).

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