# REVIEW



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# Adaptive sampling in ecology: Key challenges and future opportunities

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### **Abstract**

- 1. Traditional ecological monitoring employs fixed designs, which do not vary over the survey duration. Adaptive sampling, whereby the data already collected informs a sampling design which changes over the course of the study, can provide a more optimal and flexible survey design but is little used in ecology.
- 2. We aim to provide an introduction to adaptive sampling for ecologists. We review previous literature and highlight examples of both empirical adaptive approaches, such as adaptive cluster sampling, and more novel model-based adaptive methods.
- 3. To conceptualise the process of adaptive sampling we identify four key stages: choice of data, definition of a criterion, selection of new sampling occasions and sampling activity. We discuss each stage in turn and focus on the decisions ecologists need to consider in order to successfully implement an adaptive sampling strategy. We include a full walkthrough of an adaptive sampling example with code provided to demonstrate each step.
- 4. Adaptive sampling has potential advantages to ecologists but so far has had limited uptake. We review key challenges and barriers to uptake and suggest potential ways forward. We hope our paper will both increase awareness of adaptive sampling methods and provide a useful resource for ecologists considering an adaptive survey design.

# KEYWORDS

adaptive sampling, ecology, framework, monitoring, survey design

# | INTRODUCTION

Long-term, large-scale monitoring provides a crucial source of information to understand ecological status and change (Magurran et al., 2010). Using such information, models can be derived that can further elucidate how, where and why ecosystems are changing (Hubau et al., 2020; Soroye et al., 2020), including related pressures, drivers and taxonomic impacts. These data and models underpin our current knowledge and projections of

ecological systems. Ecological monitoring, defined as field-based measurements repeatedly collected over time (Lindenmayer & Likens, 2010), can take various forms and there are many factors that may determine the chosen survey design. For example: issues of cost, available resources and scientific rationale may all contribute to the design of any ecological monitoring initiative. The underlying scientific rationale, which encompasses the original hypotheses, reporting classes (i.e. the scale or categories for which inference is desired) and target population, is often regarded as

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the single most important factor to determine the monitoring design (Nichols & Williams, 2006).

Pilot surveys, often followed by power analyses, can be used to understand the trade-offs between different designs and other key features, such as statistical power, cost and overall time frame of monitoring. These help to determine the most appropriate strategy for monitoring and the locations and times of where and when future field sampling is conducted (Green, 1989). Despite this, it is usual for the design, once chosen, to be fixed throughout the duration of the scheme (e.g. Haase et al., 2018). This is generally considered a sensible and robust decision, as it ensures that the analysis of data is straight-forward, which is especially useful in the case of designbased inference (Dumelle et al., 2022). However, a design which is fixed at the start of sampling and does not change, will likely not optimally allocate resources in the future to answer questions of interest. In particular, a fixed design does not allow the data collected in initial surveys, which may be highly informative, to influence the design in future sampling occasions. Examples where data may be informative include where rare species have been sighted; and where unusual ecological conditions occur. These areas may not be adequately sampled in the original design and under adaptive sampling sufficient resources can be allocated accordingly. However, in a fixed design, the sampling strategy does not change regardless of the data collected.

Fixed designs also assume that the system of interest remains stationary over the course of a monitoring scheme. Yet, there may often be both internal and external factors that change over time. which compromise this assumption. This could mean that a scheme that was considered optimal at the start becomes less optimal or efficient throughout its duration, and therefore, is no longer sufficiently robust to answer the scientific questions of interest (Wikle & Royle, 2005). In ecological contexts, this could be problematic, as the environment of interest will often be subject to many known factors that are highly dynamic and hence non-stationary over time. For example, a landscape-scale monitoring programme that was designed to assess the impact of an agri-environment scheme on biodiversity would be compromised if farms that were initially selected as control sites, on account of not being in the scheme, subsequently joined the scheme. Analyses would then struggle to disentangle the effect of scheme on biodiversity response from any change in the control population.

Adaptive sampling breaks from the convention of optimally designing a scheme from the outset that is then fixed over time. Instead, it embraces the concept of continual learning and improvement in the design as more information becomes available in response to change in internal and external factors (Jain & Chang, 2004; Runger & Pignatiello Jr, 1991; Xu et al., 2016). For example, a survey focused on estimating the abundance of a rare species over space might direct more effort towards sites where the species was seen in the previous survey (Conroy et al., 2008). Adaptive sampling requires a decision-making framework that utilises information obtained throughout the monitoring history to determine where and when to sample in the future. This can take

place as part of an iterative or continual procedure, so that decisions about sampling design can be changed over time, informed by the data already collected.

Changing the sampling design over time based on data previously collected, contradicts some traditional conventions of monitoring design, whereby randomisation and consistency are considered to be fundamental. These two elements relate to inclusion probabilities, that is the probability that any individual observation from the population is included within the sample. With equal inclusion probabilities across the sample, the data obtained are directly representative of the target population and inference is possible across this population. In adaptive sampling approaches, where inclusion probabilities are changing over space and time, the observations are no longer necessarily directly representative of the target population. Without accounting for the changes to the design and the preferential sampling conducted, inference may therefore be biased. Although it may seem that this would create substantial challenges for data analysis, statistical methods are available to allow robust inference from adaptively sampled data. Crucially, the sampling procedure, although dynamic, can still be probabilistic and therefore retain inclusion probabilities for every observation in the sample. The key element is that although inclusion probabilities may not be even over space and time, they are known over space and time. These probabilities allow for robust inference to be drawn from a dataset collected using adaptively sampled data. In some cases, the inclusion of latent effects such as a random effect that is shared between the original and new data, may be sufficient to account for adaptive methods (Pacifici et al., 2016). In others, adaptively collected observations can be weighted using simple statistical methods that directly incorporate inclusion probabilities, such as the Horvitz-Thompson estimator (Thompson, 1992). Methods are also available for use in more complex scenarios, such as when the inclusion probabilities are not known for all observations in the dataset or when the initial data are of a completely different structure from those to be collected (Reich et al., 2018). Furthermore, in some, albeit limited, situations it is possible that no adjustment is needed to the model structure if suitable latent processes are already included (Chipeta et al., 2016; Pacifici et al., 2016). Therefore, complexities in data analysis are no longer a barrier to implementing an adaptive design.

Adaptive sampling approaches are currently routinely adopted within control systems, engineering and manufacturing (Kondratenko et al., 2022), autonomous systems (Hwang et al., 2019) and internet of things applications (Giouroukis et al., 2020), where the observations are highly dynamic with high intensity. Within ecology, the past decade has seen a proliferation of data from various sources including bioacoustic sensors, remote sensing, citizen science and eDNA. This proliferation has led to a surge in integrated analytical approaches to combine data from multiple sources. However, while there have been few specific examples considering more changeable approaches to monitoring (e.g. Callaghan et al., 2019; Flint et al., 2024; Williams et al., 2018), in the broad context, there has been relatively little attention given to generalisable approaches on how data may be collected more dynamically and optimally over

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time to provide the best use of effort either for individual monitoring networks or within integrated monitoring systems.

In what follows, we aim to provide an accessible introduction to adaptive sampling within ecology and raise awareness of the potential to design more flexible and adaptive long-term monitoring initiatives. We define four key stages of adaptive sampling and consider the decisions required at each stage. We explore opportunities for adaptive sampling and highlight a number of successful implementations in the literature where adaptive designs have led to better inference and more efficient monitoring. We also discuss challenges to using an adaptive design and identify future research opportunities.

### 2 | ADAPTIVE SAMPLING

Adaptive sampling is the process of using prior observations to inform further sampling in order to maximise the information content provided by the data in relation to a question of interest. For a long-term ecological monitoring programme, adaptive sampling can offer significant advantages using all information collected during the sampling process up to a specific point to optimally select subsequent sampling units (Xu et al., 2016). The process is then repeated for each sampling event, optimising the data collection each time. In this sense, sampling effort is continuously redeployed according to objective decisions chosen to improve ecological inference.

Adaptive sampling fits within the framework of adaptive monitoring (Lindenmayer & Likens, 2010). Adaptive monitoring allows ecological monitoring to change over time in response to either new questions, new observations or new technologies which might all require a change in monitoring approach. We distinguish adaptive sampling here as altering data collection to answer a fixed question of interest, whereas adaptive monitoring also considers cases where the question of interest itself changes over time. Adaptive sampling overlaps conceptually with optimal design (Millard & Lettenmaier, 1986) but is distinguished by iterative use of previously collected data. Typically, in adaptive sampling, we consider that the question of interest and aim of the monitoring is predefined and does not change over the course of the sampling. Though, of course, the principles of adaptive sampling can be used within an adaptive monitoring context. Once the question has been chosen, we define four core elements of any adaptive sampling design: the choice of data, the definition of a criterion, the selection of new sampling occasions and the sampling activity (Figure 1). The ultimate aim of the adaptive sampling is to take optimal actions (usually new data collection) which most efficiently answer the question of interest.

The choice of data covers both the initial data collected prior to any adaptive sampling and any data collected subsequently. These data can differ between initial (pre-adaptive sampling) and later stages, both in terms of the adaptive changes to the design and the sampling protocol. For example, an initial occupancy survey might be followed up by an abundance survey

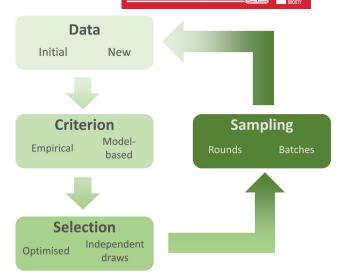


FIGURE 1 An outline of the adaptive sampling process. At the start of any scheme, initial data are used to inform where or when further sampling should be undertaken. These data are used to define a criterion that determines the conditions under which further sampling can take place. A criterion can be broadly categorised as either empirical or model-based. Empirical sampling methods use the data directly to inform where further sampling should occur; in model-based methods, we use some feature of a model derived from the initial data. Once the criterion layer is defined, we can use it to select further sampling occasions. Selection of sampling occasions can be done using a spectrum of methods, from optimised sampling at one end to independent sampling at the other. At the optimised end, all sampling occasions within a set are drawn together and the set is refined using direct optimisation or some approximation method (e.g. MCMC). At the independent end, each sampling occasion within a set is chosen independently from all other sampling occasions. An important concept in adaptive sampling is its iterative nature and how sampling should take place. Decisions are therefore required about the number of rounds over which adaptive sampling occurs, and how many samples, or batches (batch size), are taken in each one. This is often a trade-off, as each round requires the criterion and selection steps to be repeated, which could be costly and time consuming. This provides new data, which can be combined or kept separate from the initial data to restart the adaptive sampling process.

designed adaptively based on information from the first survey.

The definition of a criterion considers how the data available will be used to decide which elements of the sampling design to alter (e.g. location of observations or frequency of sampling). There are many ways in which a criterion can be constructed. Broadly speaking, approaches can be empirical, where the survey design is influenced directly by a particular (set of) observation(s); or model-based, where the design is influenced by a model derived from the data. A simple example of an empirical approach is expending

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more sampling effort in locations with no previous observations.

The selection of new sampling occasions is the process by which the criterion is used to decide the locations or times to sample new data. The criterion can be used to determine the value that any new observation would have (henceforth called the utility) and there are numerous ways in which this can be used to determine new sampling occasions from: optimal—whereby the conditional dependence of each new location is considered and hence how the utility changes once new sampling points are selected; to independent—where each new sampling occasion is selected based solely on the initial utility independently of any other new sampling point selected.

The sampling activity is the process of actively sampling the new sampling occasions and generating new data. Having selected candidate units to sample, this step typically determines how the practicalities of data collection are executed. A fundamental decision is whether all sampling units are considered individually or are split into batches to be sampled.

The four phases of adaptive sampling each require a set of decisions to be made, and the following sections consider each element in turn, highlighting important aspects to consider when implementing an adaptive design.

## 2.1 | Data

As adaptive sampling is built on the premise of utilising existing information, a set of initial data are required before one can consider future sampling events. Critically, these data are required to provide some information with which to value the benefits of sampling units across the domain of interest. These initial data might arise from an existing survey design, if adaptive sampling is employed within an ongoing monitoring effort, or might come from a pilot survey if a new adaptive monitoring scheme is started. It is not necessary that initial data are collected in the same way as the data that will be collected as part of the action phase. For example, data already collected by citizen scientists could be used as initial data to inform subsequent professional surveys (Reich et al., 2018). Initial data collected by remote sensing methods could similarly be used to inform on the ground monitoring (Wikle & Royle, 2005). Initial data are generally included in subsequent analyses, even after adaptively sampled data are collected, which may require the use of integrated models if the initial data are of a different type to subsequently sampled data (Isaac et al., 2020). In such situations, Bayesian models can be extremely useful. These have been used to include occupancy estimates from initial opportunistic data as informative priors in

the subsequent model of the structured data (Pacifici et al., 2017). The concept of using the initial data as informative priors within a Bayesian approach gives rise to the idea that initial data gathering may be from expert elicitation. This is becoming increasingly popular in ecological studies (Choy et al., 2009) and, if done appropriately, could provide a robust basis for the initial data step in an adaptive sampling framework.

It is important to note that the data phase depicted in Figure 1, is not specific to the initial data upon starting adaptive sampling. The data phase represents all data collated and known up to the current point and is therefore a pooling of data across all previous sampling occasions. In the context of adaptive sampling, it may be necessary to consider whether initial and new data should be weighted in some way. Weighting of data can potentially help to overcome any issues with bias in the early stages of data collection and may be useful prior to the next phase of adaptive sampling (Chiffard et al., 2020). However, to do so effectively requires careful tracking of data throughout the monitoring cycle and an understanding of the design decisions that have dictated why each specific sampling unit was chosen.

With all available data collated, pooled and weighting considered, the next step is to define the criterion for adaptive sampling.

### 2.2 | Criterion

Conditional on the data available, a criterion needs to be defined to decide under which conditions an action, such as making new observations, should be taken. There are many ways in which the data obtained in phase 1 could be used depending on the question of interest. For example, a criterion could be as simple as identifying regions with no existing data. Alternatively, a criterion may be based on a complex dynamic model of the initial data which predicts regions where a species is likely to be present in the future (Williams et al., 2018). This section describes some of the decisions to be considered when defining a criterion and provides examples from the ecological literature.

### 2.2.1 | Model-based versus empirical

Empirical approaches use the data collected to define where or when to collect new observations based on a trigger (type of observation, over a threshold, etc.). There are several examples of empirical adaptive processes used in ecological sampling. One particular area where adaptive sampling has a long history in ecology is in estimating the abundance of rare species. Estimating the population size of rare species is challenging and it can be important to optimise the likelihood of finding a species for a given amount of search effort as searching is often costly. Adaptive cluster sampling (Thompson, 1990) can increase the chance of a positive observation when the ecosystem properties are patchily distributed. This approach consists of two phases: an initial

random survey followed by targeted surveys in areas neighbouring positive observations made in the first survey. This method is empirical as the decision to conduct further sampling is based on the initial data and not on a model. This approach has been used to estimate population size of rare species by targeted search effort (e.g. Philippi, 2005). The induced bias in the second survey can be accounted for in estimates of population parameters by including the probability of inclusion derived from the first survey (e.g. via the modified Horvitz-Thompson estimator (Horvitz & Thompson, 1952)). In their paper, Irvine et al. (2013) use a binary spatial regression model to model the occupancy of species observed along transects using adaptive cluster designs. Recent work has combined adaptive cluster sampling with (spatially explicit) occupancy modelling to estimate populations of rare species and simultaneously account for imperfect detection (Pacifici et al., 2016). Conroy et al. (2008) used an empirical adaptive sampling approach whereby detection in an occupancy survey triggered deployment of more intensive abundance surveys to estimate abundance of rare species. By jointly modelling the occupancy and abundance data obtained, they were able to obtain abundance estimates for sites not sampled in the second intensive survev

In a model-based approach, the initial data are not used directly to define a criterion. Rather, some feature of a model of the initial data is chosen as a criterion to optimise; this could be based on specific parameter values, uncertainty in one or more parameters uncertainty in the model predictions or the predictions themselves. A model-based approach can have theoretical advantages over an empirical approach. For example, an empirical approach to collect records from locations with no previous observations may lead to effort expended in areas which are already known to be outside of the suitable habitat for a species. Conversely, choosing to survey in areas of high uncertainty in model predictions should avoid this problem by utilising existing knowledge of species distributions. Furthermore, we can choose our sampling locations/times specifically to optimise a criterion of interest, meaning we can dictate exactly how our inference will benefit from future sampling. In simple cases, this optimisation can be achieved mathematically exactly. For example, we may be interested in minimising the variance across the set of estimated model parameters. An example of a direct optimisation criterion would be to use the inverse of the Fisher information matrix.

In this model-based approach to adaptive sampling, all decisions are conditional on the model specified and therefore sensitive to assumptions about it being correct and appropriate. This means that model-based adaptive sampling may be unreliable if initial data are biased or model assumptions are wrong. This could lead to compounding bias sampling issues and mis-representing large portions of the sampling domain (Callaghan et al., 2022). However, the benefit of adaptive designs is that the criterion can change to counteract these initial issues when they are discovered as the whole process embraces the concept of continuous improvement. Model-based adaptive sampling has been used in a range of contexts

and has been shown to have benefits over simple random sampling (Specht et al., 2017; Turk & Borkowski, 2005). In a recent paper, Flint et al. (2024) used a model-based approach to facilitate a valuation of new observations. Although not adopted within an iterative adaptive sampling context, their approach demonstrates the use of model features to prioritise new data collection.

# 2.2.2 | Choice of metric

With model-based adaptive sampling, there are many different possible options for the choice of optimisation metric to use. This should be determined according to the requirements and aims of the monitoring scheme itself, though there are some commonly used metrics. Broadly speaking, these can be separated into measures related to the mean of the process or to the variation around it. Suitable criteria that relate to the mean process may include optimising sampling for the presence of a particular value (e.g. a rare species; Pacifici et al., 2012); for a threshold (e.g. number of unique species; Callaghan et al., 2022); or for detecting extreme events (e.g. algal blooms; Germán et al., 2020). Detection of rare species is an important priority for conservation and there are several examples where models are used to improve the efficiency of sampling for rare species (Guisan et al., 2006). Jeliazkov et al. (2022) define 'SDM-guided' sampling for rare species as sampling in areas of high predicted probability; we would define this as an example of model-based adaptive sampling with a mean-focused criterion. In each case, the expected predicted value of the model is used as the fundamental criterion to maximise or minimise.

Minimising the uncertainty or variation in model estimates is desirable in many circumstances due to the impact this may have in terms of improving predictive power or the power to detect effects. One such example is minimising uncertainty in species distribution models to have greater confidence in species ranges. Commonly used criteria in this sense include the average predictive variance, maximum predictive variance and parameter-specific variance. Reich et al. (2018) optimised the expected misclassification rate (Brier score) in their two-stage adaptive design, whereby citizen science data was used to inform a professional survey designed to estimate species distributions. Areas with higher expected misclassification rates estimated from the citizen science data indicate areas of higher uncertainty and sampling designs were chosen that minimised this rate. The resulting locations chosen for sampling tended to be in regions outside or at the edge of areas with high predicted occupancy, with locations where citizen science data predicted high occupancy being least informative for new sampling. In some simple cases, the objective criterion can be analytically derived and optimised by standard mathematical operations. In other, more complex cases, this is not possible and alternative solutions such as MCMC sampling approaches and the use of posterior distributions may be required.

For empirical adaptive sampling designs, there is no concept of mean or variance to guide criterion choice. Instead, the criterion must be derived from some property of the observations themselves, for example, locations, times or values, for example, species counts. The majority of empirical approaches discussed above (e.g. Pacifici et al., 2016; Thompson, 1990) construct an adaptive sampling design based on the locations of occurrences, so that additional effort is expended near to existing observations. More generally, this form of adaptive sampling over-represents sampling units with a property of interest (e.g. occurrence) while still allowing unbiased estimation of parameters such as population size. Occurrence can also be a trigger in temporal designs, for example, sites may only be visited until one or more observations are made (removal design; MacKenzie & Royle, 2005).

#### 2.2.3 Model choice

In a model-based adaptive sampling design, the choice of model is key. A very basic model which estimates only a global mean and variance would provide no valuable information of use to define a criterion for adaptive sampling. A more complex model might include spatially or temporally varying covariates, an explicit spatial process and/or a temporal process. Importantly, if terms are not included in a model, and therefore not explicitly quantified, then their effect cannot be isolated for use in any criterion. For example, a model containing spatially varying covariates but no explicit spatial process, cannot directly be used to optimally determine the new locations of sampling units-information is only known in relation to the covariates (Wagner & Fortin, 2005). Instead, an indirect process must be used whereby a criterion for sampling in covariate space is defined, which is then mapped into real space. The resulting criterion will not take into account the distance between observations and could result in locations very close together all having high priority for sampling.

The structure of the chosen model will also affect the criterion, even if the model components are the same. For example, a generalised linear model (GLM) and a generalised additive model (GAM) fitted to the same covariates will produce different variance estimates due to different assumptions about linearity in covariate relationships. A GLM is parameterised using only a single parameter (representing the gradient of the relationship) to describe the relationship between response and covariate. This means that the greatest uncertainty will always be at the extremes of the covariate space as the gradient varies around the fixed point. On the other hand, GAMs do not make any assumptions about linearity and uncertainty is in relation to the coefficients of derived basis vectors. Variance can therefore, in theory, be high at any point in covariate space. Conversely, machine learning approaches such as random forests or boosted regression trees do not produce models with parameter uncertainty and therefore to extract any estimate of predictive variance requires some form of resampling and refitting of the model. If an ensemble of models is used in an uncertainty-based adaptive sampling scheme, care must be taken to ensure that uncertainty is comparable across model types and the effect of model assumptions on uncertainty are considered.

Any model-based adaptive sampling scheme will rely on the assumption that the chosen model is appropriate. For example, if distributional assumptions are made that are not met (e.g. a normal distribution assumed when the data are heavily skewed), then resulting mean and variance estimates will be biased and of minimal use in defining an adaptive sampling criterion.

#### 2.2.4 Constraints

Ecological sampling is generally subject to many practical and logistical constraints (Field et al., 2007). Constraints may include: resource limitations, access permissions at particular sites, predetermined survey seasons, availability of surveyors, volunteer uptake at particular locations and times of year and co-location requirements. In schemes reliant on volunteer recorders, further constraints could be imposed by the recording preferences of individuals. This could result in large numbers of records from locations that provide little valuable information, for example, repeated visits to already wellrecorded areas (Mondain-Monval et al., 2024). These issues can limit the feasibility of a design that will dynamically change over time by imposing additional rules and restrictions on the design options. Broadly speaking, constraints can be binary (e.g. access granted or not), categorical (e.g. high, medium or low volunteer community near site) or continuous (e.g. cost of travel to location). For adaptive sampling schemes to be viable in practical scenarios where such constraints are present, there must be some mechanism to overcome any constraints and determine a practically feasible selection of sampling units.

There are two main approaches to dealing with constraints in an adaptive sampling design, which echo similar approaches in standard sampling theory based on adapting inclusion probabilities (Firth & Bennett, 1998). Firstly, the constraints can be considered part of the criterion, such that some element is optimised with regard to constraints. For example, accessibility could be included in the criterion by down-weighting sites that are more difficult to access. In standard sampling theory, this is equivalent to adjusting inclusion probabilities, which is standard practice for issues such as incorporating legacy sites into survey design (Foster et al., 2017). In theory, all types of constraint-binary, categorical or continuous-could be dealt with in this manner. There is no prerequisite on the type of constrain for integration within the criterion to be an appropriate approach.

Alternatively, constraints can be applied after the criterion is defined, as part of the sampling phase. In this scenario, the pool of possible sampling units is diminished by excluding those that do not conform to the criteria or constraint specified. Once again, this could apply to all type of constraint-binary categorical and continuous. For example, if co-location with another survey is important, then the survey locations can be chosen using the criterion applied only to the available pool of co-located sites. Similarly, sites without permissions could be masked out of the available pool of sites as part of the action.

#### 2.3.1 Choosing sampling locations or times

Once a criterion is defined, it can be used to choose new locations or times of sampling. Generally, there is a spectrum of approaches one can consider along an axis from: selecting a set acknowledging full conditional dependence; through to independent draws of sites one at a time. If selecting a set based on conditional dependence, then a set of locations (or times) of a given size are chosen simultaneously. Choosing the entire set of sampling locations together means that new points can be considered, conditional on all other sampling points within the set. This should guarantee that the set as a whole is optimal. The disadvantage of this approach is that, because the location of each sample will affect the optimality of all other samples, it is rare that a simple analytical solution exists and a time-consuming iteration approach is required to calculate the set (e.g. Reich et al., 2018).

The alternative approach is to draw new locations independently rather than optimising the set as a whole (e.g. Pacifici et al., 2012). This approach has the advantage of being much less computationally demanding but is not guaranteed to calculate the optimal set as it does not consider how choosing one location may affect subsequent choices within the same set. By ignoring conditional dependence, independent draws may also be more likely to choose new locations which are very close to each other requiring additional constraints on minimum distances between locations to be set (Chipeta et al., 2016). For example, if the residual model variance was chosen as the criterion, and therefore new sampling locations were selected where this was high, then using independent draws could lead to a set of new sampling locations clustered around the area of high variability. Whereas the optimal approach would recognise that once one sampling point is assigned to that location, the information provided would sufficiently lower the uncertainty and any additional monitoring effort could be directed elsewhere.

Although direct optimisation is generally theoretically advantageous, it is often computationally challenging and may be too costly in many cases. Drawing locations independently is a more flexible approach, and can be easily re-calculated if, for example, the number of possible locations change, or if additional constraints are discovered. It is also possible to incorporate some notion of dependence between sites when undertaking independent draws, hence, the concept of a spectrum of approaches. An example of this would be to eliminate possible candidate sites, based on some rule, as new sites are chosen through independent draws (Box 1). In Box 1, any site within 10km of one selected by an independent draw was subsequently excluded.

# Sampling activity

#### 2.4.1 Rounds and batch size

Due to the inherently iterative nature of adaptive sampling, decisions also need to be made about how many rounds of adaptive sampling

are made and how many samples are taken per round (batch size). We define a full 'round' of adaptive sampling as all the components of Figure 1, that is, from data collection to identification of criteria for resampling and the re-sampling action. Many examples of adaptive sampling in the ecological literature include only two rounds (e.g. Pacifici et al., 2012), perhaps due to constraints associated with research project funding or field seasons. However, the number of rounds can be much higher (Xu et al., 2016), although may not be known in advance for long-term field studies. Round frequency will be determined by a number of factors including the sampling time required for each round, the length of the field season and the project aims. For example, if the aim was to use adaptive sampling to efficiently map a species distribution in space, then it would be sensible to allow a number of rounds within a time frame in which the distribution can be assumed to be stable. Each round may also require computational time for any optimisation procedure. This may be the most important constraint where data are collected continuously, for example, via a set of camera traps, but a decision must be made about how frequently to run the adaptive sampling procedure to decide on optimal trap operation (Kays et al., 2020). Balantic and Donovan (2019) describe a temporally adaptive sampling process for detecting a suite of focal species with acoustic monitoring. They found this to be advantageous when compared to fixed sampling times, which may generate 'false absences' because it is not practical to have continuous acoustic monitoring.

Within each round, the batch size, or number of samples, also needs to be considered. If there is a fixed total set of sampling effort available, then the distribution of effort between rounds and batches can be considered as its own optimisation problem (McDonald, 2003). Generally speaking, the value of adaptive sampling is usually highest with many rounds of small batches (Chipeta et al., 2016), but this may be much more costly than fewer rounds with larger batches.

# **KEY CHALLENGES**

The concept of learning from data and continuously updating the sampling process based on a specified criterion poses a number of challenges. We briefly describe some of these in the following sections.

#### 3.1 **Preferential sampling**

In adopting an adaptive sampling design, all modelling assumptions associated with randomised sampling routines are violated and design-based inference is no longer possible. Sampling is now specifically targeted towards certain areas and/or visit times, which means that the raw sampling data are no longer representative of the target population. Therefore, to achieve unbiased results and retain outputs representative of the target domain, this targeting must be accounted for within the modelling framework. This issue is known in statistical terms as preferential sampling (Diggle et al., 2010). Preferential sampling is a particular issue when the criterion of interest is chosen based on the mean of the process, for

### BOX 1

Here, we provide an example of using adaptive sampling to improve our knowledge of the distribution of a single simulated species (Figure 2). A full walkthrough of the code to carry out adaptive sampling can be found in the Supporting Information and all codes is available here: https://github.com/NERC-CEH/adaptive\_sampling\_walkthrough/blob/main/README.md. All data are freely available online. In this example, we have records of a species in Great Britain (GB), but we do not believe that we have sampled its entire range. We therefore wish to improve our knowledge about its distribution by recording more observations. Importantly, we have some existing (initial) data which we want to use to optimise subsequent sampling—that is, use adaptive sampling to make our recording more efficient.

We first need to determine our sampling priorities, our criterion, which can be done in several ways; we consider two approaches. In the first, we use the data to inform further sampling directly-empirical adaptive sampling. Specifically, in our example, we identified all areas across GB in which there were no records and prioritised these regions for sampling. In the second approach, we based our sampling priorities on the outputs of a model-model-based adaptive sampling. We fitted a General Additive Model (GAM) to predict the presence of the species across GB. We then extracted the standard error of these predictions to determine where the models were most uncertain. Prioritising sampling in the regions of highest uncertainty should improve model performance and therefore our knowledge of the species' distribution.

Once our criterion has been defined, we then need to select where our sampling will take place from our criterion layers. Choosing sampling locations can be done in different ways but can broadly be put on a spectrum from independent draws at one end, to full conditional optimisation at the other. For the independent draws method, we sampled locations independently from one another, without accounting for the utility of each sampling occasion. For the empirical sampling criterion, this involved randomly selecting locations from the unvisited locations identified in the previous step. For the model-based sampling criterion, we selected the areas from an ordered list headed by the highest standard error in the model predictions down to the lowest standard error.

Independent selection can result in a clustered distribution of sampling locations, which might not be desirable in the case of understanding species distributions, though there are cases (e.g. estimating covariance parameters) where this may be a desirable property. Instead, we might be interested in spreading our recording over a wider area. In this case, optimising our sampling locations might be preferential. For this, we ensured that no two adaptively sampled locations were within 10 km of each other. In the model-based approach, we selected the area with the highest uncertainty, removed all points within 10km and then selected the next area with the highest uncertainty from the remaining locations. It is important to note that this is only one method of optimising further sampling occasions, and is a mix between independent draws and true optimisation. In true optimisation, sampling occasions are chosen as a set and optimality determined by adding, deleting or exchanging sampling occasions within that initial set. After each change, the criterion is recalculated and this process continues until no further benefit is seen. In designs involving many sampling occasions, as is the case with many SDMs applications, for example, this becomes computationally intractable and so approximation algorithms are used (Reich et al., 2018) or the independent draws methods. Therefore, optimisation of sampling locations might not be suitable in many cases.

The final decision in any adaptive sampling scheme is to determine how many rounds of sampling and the batch size (number of data points) in each. This is usually dependent on design-specific constraints. For example, it might be that sampling can only take place in a single season or that there are only enough professional recorders to sample at a certain number of sites. Once sampling has been completed, the new data are usually combined with the initial data to answer the question of interest or continue the iterative adaptive sampling process. In our example, four rounds of adaptive sampling are applied.

example, targeting areas with high predicted probability (Chiffard et al., 2020; Pacifici et al., 2012).

There are different approaches to accounting for preferentially sampled data (e.g. Diggle et al., 2010; Gelfand et al., 2012; Vedensky et al., 2022) that ultimately depend on the type of analyses, and hence questions, one is interested in. While much has been written in the statistical literature in this area and many tools are available within standardised software packages, it is inevitably the case that any modelling/analyses conducted will be more complex and computationally demanding than the scenario of randomised data collection. Pennino et al. (2019) provide an example of fitting species distribution models using preferentially sampled data, which relies on fitting a two-part model. In this, the first component is used to account for the sampling locations and then the species observations are accounted for in the second component. With a randomised design, only the second component would be required, and therefore, a much simpler modelling approach. However, in some cases, it can be shown that preferential sampling is not an issue for adaptive designs (Chipeta et al., 2016; Pacifici et al., 2016), so the risk of preferential sampling will vary

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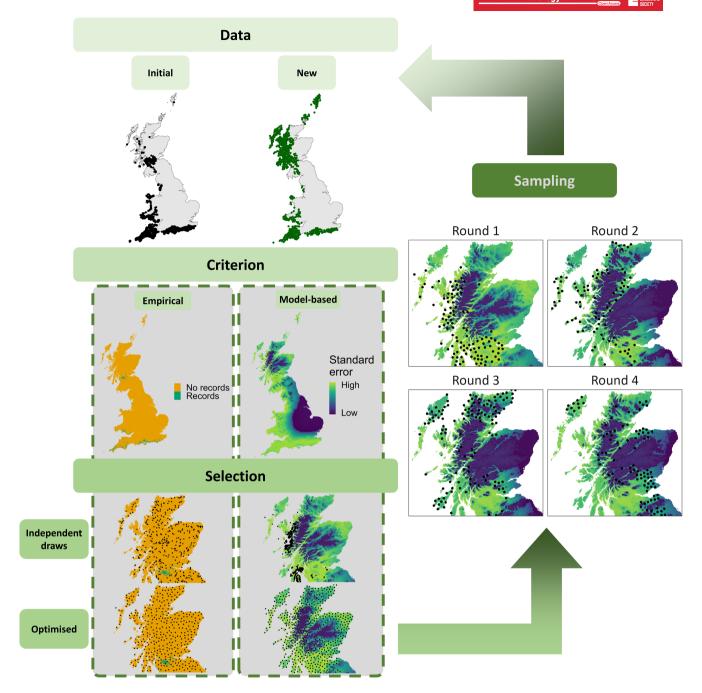


FIGURE 2 Improving our knowledge of species distributions using adaptive sampling. This figure illustrates the four core elements of adaptive sampling using the case of SDMs. The entire process is described in Box 1; the code used to carry out adaptive sampling and produce the images presented here can be found in the Supporting Information.

depending on the adaptive methodology chosen. In addition, initial data are usually analysed alongside any subsequently collected adaptively sampled data which can help to mitigate any potential biases (Reich et al., 2018).

# 3.2 | Biased or imperfect data

Ecological data are often subject to imperfect detection and some data sources, particularly those that are unstructured and rely on

volunteers, may be biased in relation to time and/or space. It can be challenging to integrate adaptive sampling into this type of monitoring scheme because the original data is itself not necessarily representative of the domain of interest (Boyd et al., 2023; Callaghan et al., 2022). In this scenario, it is possible for adaptive sampling to compound bias and to make robust inference problematic. To apply adaptive sampling in this context, it is essential that bias can be accounted for within the modelling approach. Ecologists therefore need to consider how adaptive sampling can be applied in these contexts and how biases in data can be

accounted for in models incorporating both original and new adaptively sampled measurements. The critical difference between bias in the data and preferential sampling as referred to in the previous section, is that preferential sampling resulting from adaptive sampling is *known* and can be accounted for. If the source of bias in data is unknown and cannot be reasonably accounted for, then robust inference can be challenging.

# 3.3 | Multiple objectives

Whilst it is typical for adaptive sampling to consider a single goal or property to optimise, for example, the number of observations of a species or the uncertainty in a distribution model, it may be the case that there exist multiple criteria or specific metrics that one wishes to optimise new sampling for. This can often be the case for schemes that are designed with multiple objectives from the outset. For example, many ecological surveys collect data on multiple species using the same sampling design, and therefore, may wish to choose new sampling locations that are optimal across a number of species. There are two potential options for multiple objective optimisation of this sort: The first is to condense all information from across the multiple criteria into a single metric using some form of weighting or aggregation process; the second is to treat the multiple criteria in a multivariate manner and optimise across all metrics using gradient descent (Mandic, 2004) or Pareto front-based (Ngatchou et al., 2005) approaches. For monitoring schemes with multiple objectives, it may be that a single, optimal design is difficult to establish. In some circumstances, hybrid designs with a standard, fixed design component and an additional adaptive component may therefore be most appropriate for ecologists. Williams et al. (2018) notes that hybrid designs are also helpful because design-based estimates can still be easily obtained from the non-adaptive component.

# 3.4 | Dynamic systems

Classical adaptive sampling designs may typically assume that the underlying ecological property of interest, for example, species distributions, remain static over the time period of interest. However, adaptive designs can be particularly useful when the ecological property is changing, for example, during a range expansion. In such scenarios, it is important to allocate sampling effort efficiently to capture the movement of a spreading population and increase the accuracy of prediction into future time steps. Dynamic sampling extends the concept of model-based adaptive sampling to involve a forecasting step, so that optimal allocation of survey effort is based on predictions of the ecological property at a future point in time (Williams et al., 2018). Dynamic sampling designs can also incorporate information about temporal autocorrelation, so that if temporal autocorrelation is high, then sites are not visited in consecutive years (Wikle & Royle, 2005).

Optimising both where and when samples are taken is more complicated than optimising either aspect in isolation. Optimising across only one of these elements necessitates an assumption of stationarity with respect to the other. Examples of this would be assuming that the spatial distribution of a species is not changing over time or that the temporal dynamics of how species abundance is changing are not varying over space. The complexity of monitoring over time and space is particularly problematic when the system or response of interest is itself changing over time and space. In such circumstances, it is possible that an adaptive sampling approach captures the ecosystem state at different stages. This may compromise the benefits of targeting the sampling via an adaptive approach because sampling at any point in time is based on what was known before that point. If the system was in a different state previously, then what was considered optimal/desirable sampling practice at that point may no longer be so if the system has changed. When stationarity cannot be assumed over space or time, it is therefore often recommended (Williams et al., 2018) that a hybrid monitoring approach, where a proportion of the sample is adaptively sampled (hence targeted) and a proportion that is consistent over time according to an original design philosophy is considered.

# 4 | BARRIERS TO UPTAKE

Adaptive sampling in ecology has been proposed for over 30 years yet is still not a mainstream concept and not widely applied within ecological monitoring (Jeliazkov et al., 2022). Traditional sampling designs often centre on consistency through time to facilitate data analysis and inference. Adaptive sampling directly contradicts this principle, meaning ecologists might be reluctant to use it despite evidence for its benefit (Xu et al., 2016). Indeed, it is possible that ecologists are uncertain about how to analyse adaptively collected data, even though in many cases these can be relatively simple to implement. This could be remedied through the input of statisticians in the design and analysis phases, although this can be costly or difficult to obtain. It is not necessarily the case that using adaptive sampling will complicate analyses. The proposed approach of Thompson (1990) relied on using inclusion probabilities to weight observations to produce an unbiased estimator. Such approaches are not specific to adaptive sampling and would be required if any type of targeting was included in the design phase (Horvitz & Thompson, 1952). However, the mathematics behind those approaches can be impenetrable for ecologists, and therefore, the additional analytical effort required for adaptive sampling could provide enough of a barrier to uptake. Additionally, this analysis would rely on an ability to track the design information, hence inclusion probabilities, over the course of the monitoring lifetime. A changing design, which may be coordinated across many different implementation groups, could mean tracking this information is much more difficult. Therefore, analytical approaches based on known inclusion probabilities may not be appropriate.

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Considering an alternative design with equal inclusion probabilities though, such as simple random sampling, an adaptive sampling approach could significantly change the proposed analysis and lead to extra work. What may have been simple design-based estimators may need to be changed to account for the preferential sampling, as previously explained. While this may sometimes be as seemingly simple as updating a standard GLM to a spatially explicit GLM, this requires significantly more quantitative skill. However, generally the analytical barriers are rapidly lowering with advancements in computing and spatial statistics. A suite of modelling approaches now exist to account for the preferential or non-ignorable sampling designs. The challenge remains, though, for there to be more applications and further guidance to aid practitioners.

Where adaptive sampling has been considered, logistical issues have often been cited as a problem. For example, in some adaptive sampling schemes, it can be difficult to determine the total number of sampling units required, as is often the case in adaptive cluster sampling where the second round of sampling is grouped around positive results in the first survey (Turk & Borkowski, 2005). This means that the total cost and duration of the survey cannot be determined a priori (Turk & Borkowski, 2005). Additional logistical issues with adaptive sampling include management of surveyor effort and survey preparation, which may be divided up regionally or potentially subcontracted to different organisations. Management of survey resources and preparation is far easier if the same sites are visited year on year. Issues with adaptive sampling are further complicated by the apparent context-dependence of adaptive designs. For example, Specht et al. (2017) suggest that simple random sampling is better than adaptive cluster sampling for predicting the distributions of common species than rare species. They also found that for rare species, the amount of sampling effort required depended on their detectability. When a species had high detectability, only 3-4 iterations of cluster sampling was needed; if the species was cryptic, the optimal number of iterations for complete sampling of parameter space increased to between 5 and 10 iterations. Therefore, the optimal sampling design is likely dependent on the characteristics of the species of interest. Pilot studies intending to inform adaptive schemes should therefore aim to determine key ecological characteristics such as detection probability (Specht et al., 2017).

Implementing adaptive designs could also affect the overall value of a monitoring scheme. Adaptive sampling requires a welldefined hypothesis or objective, as this determines the criterion layer from which to sample. Only when the aims and objectives are clearly articulated can one consider objective, adaptive sampling design. General surveillance sampling schemes are often established with generic goals, focussing on obtaining as diverse information as possible about a study system. This is particularly true for longer term schemes, meaning that specifying a hypothesis and methodology for adaptive sampling could close other interesting avenues. Furthermore, simulation studies have suggested that the benefits of adaptive sampling are greatest after multiple iterations (Chiffard et al., 2020; Chipeta et al., 2016). In reviewing papers using the methodology of Guisan et al. (2006) (mean-criterion model-based

adaptive sampling), Chiffard et al. (2020) found that as of 2019, only two papers citing the Guisan paper implemented iterative field (based) adaptive sampling (out of >450 citations at that time). This suggests that for many studies, long-term implementation of adaptive sampling might be difficult. Still, in cases where there is a specific goal, adaptive sampling could provide a significant benefit over standard sampling protocols (Turk & Borkowski, 2005).

### CONCLUSIONS

An adaptive sampling approach to monitoring provides a framework to enable ecologists to optimise their survey designs. In this paper, we have provided an overview of the adaptive sampling framework, including the four core elements and the key considerations of each. In addition, we have outlined how each of these elements provides a mechanism for sampling designs that learn and evolve to ensure that the data generated are able to optimally answer the scientific questions of interest. This contrasts with fixed designs whereby any change or learning from the data is ignored and not considered within the data generation process. This can lead to suboptimal designs as the survey progresses and, in extreme cases, can significantly compromise inferential ability. Adaptive sampling therefore provides an attractive option to ensure appropriate statistical power is maintained throughout a survey's lifetime. Similarly, adaptive sampling has the potential to reduce the overall cost of ecological sampling through increasing the information value of each observation (as also remarked by Flint et al., 2024). We summarise some of the key attributes of an adaptive sampling design in Table 1. The framework we have outlined is appropriate for both new schemes and for existing schemes. However, there is no requirement to continue with an adaptive sampling approach throughout the duration of a monitoring scheme. That, one could argue, is the whole ethos of adaptive sampling—that the sampling design is changeable according to what best suits the requirements of the scheme.

Our adaptive sampling framework exposes the requirement of a criterion to use as the basis for adaptive sampling. This criterion must relate to the question of interest for monitoring to be considered 'optimal'. Ecologists therefore need to be clear on the goals of monitoring and the scientific questions of interest. In many largescale ecological surveys, there may, however, be multiple questions of interest. Pragmatic approaches are therefore needed to ensure that any adaptive design does not limit the ability to answer all questions of interest. In other words, adaptive sampling schemes need to avoid the scenario whereby data collection has been optimised for one specific question of interest but has reduced the ability to answer any other question or report any other findings from the data. In scenarios where there are multiple and, potentially, diverse goals for the monitoring scheme, mixed designs could be considered. In these, a proportion of the total sample is subject to adaptive sampling and the remaining proportion following a fixed design.

There are many different approaches to adaptive sampling and various decisions that can be made. Practitioners should be careful

	Open Access SOCIETY	
	Non-adaptive sampling	Adaptive sampling
Clear question of interest	Required, fixed during the duration of the monitoring scheme	Required, fixed during the monitoring scheme unless adaptive monitoring is also occurring
Metric, or indicator, of interest	Single or multiple	More complex if multiple metrics are measured
Study design	Fixed during the duration of the monitoring scheme	Can change during the duration of the monitoring scheme based on data collected
Number of sampling units	Known and generally fixed during the duration of the monitoring scheme	May not be known at the start of the study, may vary over the duration of the monitoring scheme
Statistical power	May be estimated prior to sampling and rarely revisited	Power could be used as a basis for allocating effort and therefore would be maximised throughout the duration of the scheme
Time frame	Single or multiple sampling rounds	Most effective over multiple sampling rounds
Stationarity assumptions	May or may not make stationarity assumptions	More difficult to adopt (and analyse data from) if stationarity cannot be assumed between sampling rounds
Availability of existing data	Not required	Required, either pre-existing or collected as part of a pilot sampling round
Data analysis	Usually straightforward and linked to initial design	Requires a more complex analysis, but tools are widely available
Cost effectiveness	Fixed designs may be less cost effective	Can be more cost effective via adaptive deployment of resources
Flexibility	Low or non-existent	High, can adapt to changing monitoring requirements

TABLE 1 Summary of key differences between adaptive and non-adaptive sampling.

to consider which approach best suits their problem (e.g. a model-based approach or an empirical approach) and the decisions will be informed by both the nature of the question and logistical constraints (e.g. there may not be enough time to run a full optimisation procedure each time new sampling should take place). We have provided ecologists with an overview of the critical decisions needed within each element of an adaptive sampling design.

There are, however, challenges in adopting an adaptive sampling design, which we have also outlined within this paper. It is likely that many of the existing challenges are detracting ecologists from embracing adaptive designs despite the potential benefits. The most critical factor hindering uptake is likely to be the availability of methods to accommodate data obtained in this way. While the core methodological approaches exist, it is perhaps not clear to practitioners what these methods are. More examples and specific guidance of the analytical phase is therefore required. Further research is also required to consider how adaptive sampling can be used in the context of citizen science schemes, which are increasingly prominent in large-scale ecological surveys. For example, consideration of how imperfect adaptive sampling (i.e. if recorders visit only some of the desired locations) might affect the data, models and inference (Mondain-Monval et al., 2024).

Our paper has aimed to both increase awareness of the potential adaptive sampling has to improve the efficiency of ecological surveys, and to provide an overview of the decision-making process needed to implement adaptive sampling techniques.

### **AUTHOR CONTRIBUTIONS**

Peter A. Henrys and Susan G. Jarvis conceived the ideas and designed methodology; Thomas O. Mondain-Monval simulated and analysed the data; Peter A. Henrys and Susan G. Jarvis led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

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# CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

# PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14393.

# DATA AVAILABILITY STATEMENT

All the data used in this paper are freely available online. These are the UKCEH Landcover Map 2015 1km percentage aggregate class (Rowland et al., 2017; https://catalogue.ceh.ac.uk/documents/7115bc48-3ab0-475d-84ae-fd3126c20984), and climate

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and elevation data at 30s resolution provided by WorldClim (Fick & Hijmans, 2017; https://www.worldclim.org/data/worldclim21. html). All the code, and the links to the datasets used, can be found here: https://github.com/NERC-CEH/adaptive\_sampling\_ walkthrough/blob/main/README.md. Code and data available via Zenodo at: https://doi.org/10.5281/zenodo.12742175 (Henrys et al., 2024).

### STATEMENT ON INCLUSION

This was a purely theoretical and simulation-based study and did not consider diversity.

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### REFERENCES

- Balantic, C., & Donovan, T. (2019). Temporally adaptive acoustic sampling to maximize detection across a suite of focal wildlife species. Ecology and Evolution, 9(18), 10582-10600.
- Boyd, R. J., Powney, G. D., & Pescott, O. L. (2023). We need to talk about nonprobability samples. Trends in Ecology & Evolution, 38, 521-531.
- Callaghan, C. T., Bowler, D. E., Blowes, S. A., Chase, J. M., Lyons, M. B., & Pereira, H. M. (2022). Quantifying effort needed to estimate species diversity from citizen science data. Ecosphere, 13(4), e3966.
- Callaghan, C. T., Poore, A. G., Major, R. E., Rowley, J. J., & Cornwell, W. K. (2019). Optimizing future biodiversity sampling by citizen scientists. Proceedings of the Royal Society B: Biological Sciences, 286(1912), 20191487.
- Chiffard, J., Marciau, C., Yoccoz, N. G., Mouillot, F., Duchateau, S., Nadeau, I., Fontanilles, P., & Besnard, A. (2020). Adaptive nichebased sampling to improve ability to find rare and elusive species: Simulations and field tests. Methods in Ecology and Evolution, 11, 899-909. https://doi.org/10.1111/2041-210X.13399
- Chipeta, M. G., Terlouw, D. J., Phiri, K. S., & Diggle, P. J. (2016). Adaptive geostatistical design and analysis for prevalence surveys. Spatial Statistics, 15, 70-84.
- Choy, S. L., O'Leary, R., & Mengersen, K. (2009). Elicitation by design in ecology: Using expert opinion to inform priors for Bayesian statistical models. Ecology, 90(1), 265-277.
- Conroy, M. J., Runge, J. P., Barker, R. J., Schofield, M. R., & Fonnesbeck, C. J. (2008). Efficient estimation of abundance for patchily distributed populations via two-phase, adaptive sampling. Ecology, 89(12), 3362-3370.
- Diggle, P. J., Menezes, R., & Su, T. L. (2010). Geostatistical inference under preferential sampling. Journal of the Royal Statistical Society: Series C: Applied Statistics, 59(2), 191-232.
- Dumelle, M., Higham, M., Ver Hoef, J. M., Olsen, A. R., & Madsen, L. (2022). A comparison of design-based and model-based approaches for finite population spatial sampling and inference. Methods in Ecology and Evolution, 13, 2018-2029. https://doi.org/10.1111/ 2041-210X.13919
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology, 37(12), 4302-4315.
- Field, S. A., O'Connor, P. J., Tyre, A. J., & Possingham, H. P. (2007). Making monitoring meaningful. Austral Ecology, 32(5), 485-491.

- Firth, D., & Bennett, K. E. (1998). Robust models in probability sampling. Journal of the Royal Statistical Society, Series B: Statistical Methodology, 60(1), 3-21.
- Flint, I., Wu, C. H., Valavi, R., Chen, W. J., & Lin, T. E. (2024). Maximising the informativeness of new records in spatial sampling design. Methods in Ecology and Evolution, 15(1), 178-190.
- Foster, S. D., Hosack, G. R., Lawrence, E., Przeslawski, R., Hedge, P., Caley, M. J., Barrett, N. S., Williams, A., Li, J., Lynch, T., & Dambacher, J. M. (2017). Spatially balanced designs that incorporate legacy sites. Methods in Ecology and Evolution, 8(11), 1433-1442.
- Gelfand, A. E., Sahu, S. K., & Holland, D. M. (2012). On the effect of preferential sampling in spatial prediction. Environmetrics, 23(7), 565-578.
- Germán, A., Andreo, V., Tauro, C., Scavuzzo, C. M., & Ferral, A. (2020). A novel method based on time series satellite data analysis to detect algal blooms. Ecological Informatics, 59, 101131.
- Giouroukis, D., Dadiani, A., Traub, J., Zeuch, S., & Markl, V. (2020). A survey of adaptive sampling and filtering algorithms for the internet of things. In Proceedings of the 14th ACM international conference on distributed and event-based systems (pp. 27-38). Association for Computing Machinery.
- Green, R. H. (1989). Power analysis and practical strategies for environmental monitoring. Environmental Research, 50(1), 195-205.
- Guisan, A., Broennimann, O., Engler, R., Vust, M., Yoccoz, N. G., Lehmann, A., & Zimmermann, N. E. (2006). Using niche-based models to improve the sampling of rare species. Conservation Biology, 20, 501-511. https://doi.org/10.1111/j.1523-1739.2006.00354.x
- Haase, P., Tonkin, J. D., Stoll, S., Burkhard, B., Frenzel, M., Geijzendorffer, I. R., Geijzendorffer, I. R., Häuser, C., Klotz, S., Kühn, I., McDowell, W. H., Mirtl, M., Müller, F., Musche, M., Penner, J., Zacharias, S., & Schmeller, D. S. (2018). The next generation of site-based long-term ecological monitoring: Linking essential biodiversity variables and ecosystem integrity. Science of the Total Environment, 613, 1376-1384. https://doi.org/10.1016/j.scitotenv.2017.08.111
- Horvitz, D. G., & Thompson, D. J. (1952). A generalization of sampling without replacement from a finite universe. Journal of the American Statistical Association, 47(260), 663-685.
- Hubau, W., Lewis, S. L., Phillips, O. L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., Daniels, A. K., Ewango, C. E., Fauset, S., Mukinzi, J. M., & Sheil, D. (2020). Asynchronous carbon sink saturation in African and Amazonian tropical forests. Nature, 579(7797), 80-87.
- Hwang, J., Bose, N., & Fan, S. (2019). AUV adaptive sampling methods: A review. Applied Sciences, 9(15), 3145.
- Irvine, K. M., Thornton, J., Backus, V. M., Hohmann, M. G., Lehnhoff, E. A., Maxwell, B. D., Michels, K., & Rew, L. J. (2013). A comparison of adaptive sampling designs and binary spatial models: A simulation study using a census of Bromus inermis. Environmetrics, 24(6), 407-417.
- Isaac, N. J., Jarzyna, M. A., Keil, P., Dambly, L. I., Boersch-Supan, P. H., Browning, E., Freeman, S. N., Golding, N., Guillera-Arroita, G., Henrys, P. A., & Jarvis, S. (2020). Data integration for large-scale models of species distributions. Trends in Ecology & Evolution, 35(1),
- Jain, A., & Chang, E. Y. (2004). Adaptive sampling for sensor networks. In Proceedings of the 1st international workshop on data management for sensor networks: In conjunction with VLDB 2004 (pp. 10-16). Association for Computing Machinery.
- Jeliazkov, A., Gavish, Y., Marsh, C. J., Geschke, J., Brummitt, N., Rocchini, D., Haase, P., Kunin, W. E., & Henle, K. (2022). Sampling and modelling rare species: Conceptual guidelines for the neglected majority. Global Change Biology, 28, 3754-3777. https://doi.org/10.1111/ gcb.16114
- Kays, R., Arbogast, B. S., Baker-Whatton, M., Beirne, C., Boone, H. M., Bowler, M., Burneo, S. F., Cove, M. V., Ding, P., Espinosa, S., & Gonçalves, A. L. S. (2020). An empirical evaluation of camera trap

- study design: How many, how long and when? Methods in Ecology and Evolution, 11(6), 700-713.
- Kondratenko, Y. P., Kuntsevich, V. M., Chikrii, A. A., & Gubarev, V. F. (Eds.). (2022). Advanced control systems: Theory and applications. CRC Press.
- Lindenmayer, D. B., & Likens, G. E. (2010). The science and application of ecological monitoring. Biological Conservation, 143(6), 1317-1328.
- MacKenzie, D. I., & Royle, J. A. (2005). Designing occupancy studies: General advice and allocating survey effort. Journal of Applied Ecology, 42, 1105-1114.
- Magurran, A. E., Baillie, S. R., Buckland, S. T., Dick, J. M., Elston, D. A., Scott, E. M., Smith, R. I., Somerfield, P. J., & Watt, A. D. (2010). Longterm datasets in biodiversity research and monitoring: Assessing change in ecological communities through time. Trends in Ecology & Evolution, 25(10), 574-582.
- Mandic, D. P. (2004). A generalized normalized gradient descent algorithm. IEEE Signal Processing Letters, 11(2), 115-118.
- McDonald, T. L. (2003). Review of environmental monitoring methods: Survey designs. Environmental Monitoring and Assessment, 85, 277-292.
- Millard, S. P., & Lettenmaier, D. P. (1986). Optimal design of biological sampling programs using the analysis of variance. Estuarine, Coastal and Shelf Science, 22(5), 637-656.
- Mondain-Monval, T., Pocock, M., Rolph, S., August, T., Wright, E., & Jarvis, S. (2024). Adaptive sampling by citizen scientists improves species distribution model performance: A simulation study. Methods in Ecology and Evolution, 15(7), 1206-1220. https://doi.org/10.1111/ 2041-210X.14355
- Ngatchou, P., Zarei, A., & El-Sharkawi, A. (2005). Pareto multi objective optimization. In Proceedings of the 13th international conference on, intelligent systems application to power systems (pp. 84–91). IEEE.
- Nichols, J. D., & Williams, B. K. (2006). Monitoring for conservation. Trends in Ecology & Evolution, 21(12), 668-673.
- Pacifici, K., Dorazio, R. M., & Conroy, M. J. (2012). A two-phase sampling design for increasing detections of rare species in occupancy surveys. Methods in Ecology and Evolution, 3(4), 721–730.
- Pacifici, K., Reich, B. J., Dorazio, R. M., & Conroy, M. J. (2016). Occupancy estimation for rare species using a spatially-adaptive sampling design. Methods in Ecology and Evolution, 7(3), 285–293.
- Pacifici, K., Reich, B. J., Miller, D. A. W., Gardner, B., Stauffer, G., Singh, S., McKerrow, A., & Collazo, J. A. (2017). Integrating multiple data sources in species distribution modeling: A framework for data fusion. Ecology, 98, 840-850. https://doi.org/10.1002/ecy.1710
- Pennino, M. G., Paradinas, I., Illian, J. B., Muñoz, F., Bellido, J. M., López-Quílez, A., & Conesa, D. (2019). Accounting for preferential sampling in species distribution models. Ecology and Evolution, 9(1),
- Philippi, T. (2005). Adaptive cluster sampling for estimation of abundances within local populations of low-abundance plants. Ecology, 86(5), 1091-1100.
- Reich, B. J., Pacifici, K., & Stallings, J. W. (2018). Integrating auxiliary data in optimal spatial design for species distribution modelling. Methods in Ecology and Evolution, 9(6), 1626-1637.

- Rowland, C. S., Morton, R. D., Carrasco, L., McShane, G., O'Neil, A. W., & Wood, C. M. (2017). Land cover map 2015 (1 km percentage aggregate class, N. Ireland). NERC Environmental Information Data Centre. https://doi.org/10.5285/362feaea-0ccf-4a45-b11f-980c6 b89a858
- Runger, G. C., & Pignatiello, J. J., Jr. (1991). Adaptive sampling for process control. Journal of Quality Technology, 23(2), 135-155.
- Sorove, P., Newbold, T., & Kerr, J. (2020), Climate change contributes to widespread declines among bumble bees across continents. Science, 367(6478), 685-688.
- Specht, H. M., Reich, H. T., Iannarilli, F., Edwards, M. R., Stapleton, S. P., Weegman, M. D., Johnson, M. K., Yohannes, B. J., & Arnold, T. W. (2017). Occupancy surveys with conditional replicates: An alternative sampling design for rare species. Methods in Ecology and Evolution, 8(12), 1725-1734.
- Thompson, S. K. (1990). Adaptive cluster sampling. Journal of the American Statistical Association, 85(412), 1050-1059.
- Thompson, S. K. (1992). Sampling. Wiley.
- Turk, P., & Borkowski, J. J. (2005). A review of adaptive cluster sampling: 1990-2003. Environmental and Ecological Statistics, 12, 55-94. https://doi.org/10.1007/s10651-005-6818-0
- Vedensky, D., Parker, P. A., & Holan, S. H. (2022). A look into the problem of preferential sampling through the lens of survey statistics. The American Statistician, 77(3), 313-322. https://doi.org/10.1080/ 00031305.2022.2143898
- Wagner, H. H., & Fortin, M. J. (2005). Spatial analysis of landscapes: Concepts and statistics. Ecology, 86(8), 1975-1987.
- Wikle, C. K., & Royle, J. A. (2005). Dynamic design of ecological monitoring networks for non-Gaussian spatio-temporal data. Environmetrics: The Official Journal of the International Environmetrics Society, 16(5), 507-522.
- Williams, P. J., Hooten, M. B., Womble, J. N., Esslinger, G. G., & Bower, M. R. (2018). Monitoring dynamic spatio-temporal ecological processes optimally. Ecology, 99(3), 524-535.
- Xu, Y., Choi, J., Dass, S., & Maiti, T. (2016). Bayesian prediction and adaptive sampling algorithms for mobile sensor networks: Online environmental field reconstruction in space and time. Springer International Publishing.

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