Remote sensing of bird communities in the Peruvian Amazon: evaluating Landsat predictors for biodiversity monitoring

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1 Abstract

Over one-third of the Amazon rainforest has been lost or degraded through human activities. While Earth observation satellites effectively monitor forest cover, assessing the impacts of degradation on biodiversity at large scales remains challenging. We analysed 3,129 bird surveys conducted over 16 years in the Tambopata Forest, south-eastern Peru, to evaluate whether remote sensing (RS) variables derived from Landsat imagery can predict variation in bird community composition. We compared the performance of RS-based predictors with traditional habitat descriptors in modelling the occurrence probabilities of 135 commonly recorded bird species. Models using Landsat reflectance outperformed those based on habitat data for predicting species occupancy (mean AUC = 0.68 vs 0.58) and achieved high predictive accuracy (AUC > 0.7) for more species (49 vs 20). However, low detection rates limited the ability of all models to estimate true community composition and to detect temporal change. To address this, we recommend survey designs that prioritise greater replication at fewer sites, thereby improving detection rates and the power to monitor biodiversity trends. Our findings highlight the potential for integrating satellite-based environmental variables with improved survey designs to enhance biodiversity monitoring in tropical forests.

2 Introduction

Tropical forests are the most biodiverse areas on Earth (1,2), and support over a billion people with food, materials, and services (3). They also play a key role in the global carbon cycle, accounting for half of terrestrial uptake and two-thirds of forest carbon sinks in biomass, soil, and deadwood (4,5). However, clear-cut logging and commercial agriculture are altering or completely destroying forest habitats. This is evidenced by the fact that over 17% of the Amazon Basin, the world's largest continuous tropical forest, has been deforested and 38% of the remaining area has been degraded (6–8).

Conservation strategies, such as the Reducing Emissions from Deforestation and Degradation (REDD+) initiative, have generally reduced deforestation, enhanced carbon stocks, and improved sustainable forest management (9–11). However, despite the amount of tropical forest falling under protection, half of the world's tropical forest reserves continue to lose taxonomic and functional biodiversity due to disturbances beyond forest loss (12,13). The loss of forest cover can be used to estimate the level and location of carbon loss and is routinely mapped in near real-time (14), but to assess the efficacy of biodiversity conservation strategies, such as REDD+, beyond forest cover conservation, it is necessary to ascertain the current condition of biodiversity within the ecosystem and where and how it changes in the future (15–17).

Ecosystem structure is often described by the type, quantity and distribution of its components (18). However, categorical elements such as intact, logged, secondary, plantation, can be ambiguous, subjective, and require prior knowledge to define them (19,20). Despite any *a priori* assumptions, the selected elements may not be the most effective descriptors of an ecosystem's condition. In this regard, essential biodiversity

variables, including species distribution, abundance, and community composition, have been proposed as additional criteria to monitor (21,22). Thus, assessing forest health and biodiversity change requires monitoring that goes beyond simply quantifying deforestation levels. Satellite remote sensing (RS) cannot directly see essential biodiversity variables, but it allows for the measurement of deforestation along with land cover and habitat structure (14). RS can also provide broader, scalable environmental descriptors, alternative to field surveys, that act as proxies for essential biodiversity variables, for example, ecological diversity, phenology and physiology (23–26). Continuous remotely sensed variables have also been shown to be better than land class at describing plant species richness and diversity (27). RS surface reflectance values can therefore be used to infer vegetation and environmental structure as continuous gradients, rather than discrete categories, over a region of interest. This approach avoids the need to pre-define habitat classes that may overlook important ecological variation and reduces the mismatch between habitat classification and the scale at which they can be measured. While RS variables can infer potential structure and ecological richness, there is little understanding of how they relate to ecological communities within forests (28–30).

Thus, the measurement of structure or deforestation alone provides only a partial description of an environment's condition, but faunal biodiversity can regulate forest dynamics (12) and be used as an indicator of ecosystem state (31,32). Many studies have shown that land use and vegetation structure influence the biodiversity of an area. For example, dung beetle community composition and soil bioturbation are influenced by the intensity of logging within tropical forests and the spatial scale at which it is measured (33). Similarly, the richness and biological function of mammal communities are impacted by proportional levels of deforestation and the resulting size of forest patches in Atlantic Amazonian forests (34).

Furthermore, insect community richness and composition have been shown to respond to and reflect forest structure, forest composition, plant diversity and forest age (35–38). Finally, the structure of bird communities has been used both to assess the effectiveness of reforestation (39), and to show that they are negatively affected by patch size reduction within the Brazilian Amazon (40).

However, the biodiversity surveys required to adequately monitor indicator taxa are time consuming and expensive, thus limiting the effective area that can be monitored in space and time (41,42). Nevertheless, results from biodiversity surveys can be linked in statistical models with RS descriptors of the Earth's surface, to estimate community and ecosystem structure across a landscape with limited expense (43). We would expect Amazonian bird communities to be broadly influenced by the characteristics of the forest in which they occur, and if changes in forest structure led to changes in bird communities, we would expect remotely sensed surface reflectance values to correlate with this.

Furthermore, the continually updated nature of RS data could allow for this method to be used in ongoing monitoring to detect changes in community structure. As such, lastly we explore how the number of survey stations and replicate visits affects the power to detect change, helping to guide efficient survey design. By bringing these elements together, we aim to provide a practical tool for policy makers and ecologists to assess the successes and failures of management strategies, and to support decisions about financial incentives.

3 Methods

3.1 Study area and surveys

Survey data were collected by FaunaForever (www.faunaforever.org) to monitor species diversity across landscapes in the Madre de Dios region, near the Tambopata River and Puerto Maldonado in south-eastern Peru (Figure 1). Researchers and volunteers conducted bird surveys at 637 stations between 2004 and 2020. The stations were clustered around 25 centres that were located between 1.5km and 170km apart. Within centres, stations were between 200m and several kilometres apart and surveyed one to 35 times (median = 4), totalling 3,129 surveys. Stations surveyed in multiple years were treated as independent, since populations and forest structure can change over extended periods of time. This resulted in a total of 1,135 independent stations, which were surveyed between one and 21 times, with a mode of 1 survey, a median of 2 surveys and a mean of 2.9 surveys per site (SD ±2.4). Surveys used point counts (10-minute visual/audio records), or net counts (36m mist-net captures). Of 358 species identified, only 138 observed at over 10 stations were used for model training per prevalence recommendations (44).

3.2 Environmental variables

Habitat was classified by land class and forest degradation. Land classes (floodplain forest, terra firma forest, and agricultural) were based on the MapBiomas Peru Project, Collection-**1** of the Annual Land Cover and Land Use Series for Peru 2013; (MapBiomas, 2023). Forest degradation was determined from a primary forest raster using the 2000-2019 forest cover loss data set (14). Pixels were classified as primary forest if no deforestation year was given,

assuming they had remained intact. Subsequently, secondary forests were defined as areas that had undergone recorded deforestation since 2000. This classification is primary/not primary and does not differentiate between successional stages of secondary forest. The proportion of non-primary forest, equating to forest assumed to have been deforested or degraded, was calculated within three different radii around each station (1km, 2km and 5km). No cross validation was performed between the MapBiomas and Hansen datasets, so forest classifications may not align.

Of the 1135 surveys, 489 were on terra firma, 603 on floodplain and 43 on agricultural land, and 1109 were defined as being inside primary forest, and 26 in secondary forest. Elevation can influence the distribution of tropical forest bird species (46,47). However, all survey points were within the narrow range between 175m and 310m elevation, and unlikely to affect model performance; it was therefore not included in the analysis.

3.3 Satellite derived variables

Reflectance signatures at different wavelengths can be employed to assess the greenness and moisture content of vegetation, with some correlation observed between these signatures and the leaf structure of a plant (48). Reflectance and water content descriptors help describe forest canopy physiology (49). No single metric captures canopy spectral diversity (50), and the spectral characteristics and spatial scales that best capture canopy variation are unknown, so various indices were used to describe it. While many satellite platforms now provide passive optical surface reflectance data, as well as active radar reflectance, the Landsat missions were the only platforms that covered the entire period of the field surveys (Landsat-5 for 2004-2011, Landsat-7 for 2012, and Landsat-8 for 2013-2020). Frequent cloud cover over

154 tropical forests can greatly reduce the number of available images that have sufficient clarity
155 for analysis (51). To address poor visibility, annual cloud-masked, median pixel value images
156 were created in Google Earth Engine. Annual composites may mask seasonal changes such as
157 leaf flushing and fruiting cycles, or logging and burning (26,52), although phenological
158 variation in tropical forests can be lower than in some other landscapes (53). Each image
159 contained six reflectance bands, which were used to calculate seven vegetation indices: the
160 normalised difference vegetation index (NDVI), enhanced vegetation index (EVI), normalised
161 burn ratio (NBR), normalised difference water index (NDWI), and the trio of tasselled cap
162 wetness, greenness, and brightness (TCW, TCG, TCB). Both NDVI and EVI were used to detect
163 vegetation cover and vigour. NDVI was included as one of the most commonly used indices,
164 but it is prone to saturation in dense forests such as the Amazon, whereas EVI is better able
165 to penetrate the canopy and capture sub-layers. We used NBR to highlight freshly opened
166 soil, and NDWI to highlight water content within the canopy. Tasselled cap indices provide an
167 alternative way of describing reflectance and structure, and have been shown to correlate
168 with, but show more detail than, NDVI (54).
169 For each annual survey, the mean and standard deviation of pixels in each of the reflectance
170 bands and indices were calculated within 100m of each station. These 26 variables provide a
171 high-dimensional description of local vegetation reflectance. To reduce redundancy, we used
172 principal component analysis to condense the 26 variables, and the first five components,
173 explaining 96% variation in the data, were used. The distribution of the five principal
174 components and the proportion of deforestation at three scales are plotted in Figure 2, and
175 the relationship between the first two principal components with environmental descriptors
176 is shown in Figure 3.
177

178 ## 3.4 Analysis

179 To quantify species detection and assess whether bird community composition can be
180 predicted as a function of habitat or RS descriptors, we used spatial factor multi-species
181 occupancy models. Observation depends on true presence (1 = present, 0 = absent; assumed
182 constant over the year of surveillance), and the probability of detection. Detection can be
183 influenced by survey method. Mist nets at ground level tend to under-sample canopy
184 dwelling, large or less mobile species (55). Capture rates also vary with the type of net used
185 (e.g. mesh size), and netting duration. Point counts detect vocal species well, but may under-
186 sample silent or secretive species, and their effectiveness depends on background noise,
187 weather, and observer skill (56,57). Perfect detection of all species is essentially impossible.
188 Non-detection can bias covariate estimates and predictions of community composition (58).
189 However, occupancy models account for imperfect detection by estimating species
190 occurrence at each survey station, whether observed or not (59). Occupancy models also
191 provide detection probabilities for all species at all stations and the influence of survey
192 specific covariates on these probabilities (Royle and Dorazio, 2009). After fitting the model
193 and estimating species detection and occurrence probabilities, the methods of Guillera-
194 Arroita and Lahoz-Monfort (2012), were used to calculate the power of the study. The term
195 "power" is the probability of detecting a proportional reduction in occupancy between
196 surveys conducted at different times. We then calculated the survey effort required to
197 achieve a mean power across all species of 0.7, to detect a 50% occupancy reduction.
198 Although 0.8 is commonly used, our low detection rates made 0.7 a more feasible target that
199 falls within the test ranges ((Guillera-Arroita & Lahoz-Monfort, 2012). We also assessed how
200 detection power of various occupancy reductions varied with the number of stations and
201 replicate surveys, to guide survey regimes for future monitoring.

202 Four models were compared: one fitted with habitat variables, one with principal
203 components from RS reflectance, one with no occurrence variables to act as an intercept-only
204 baseline, and one RS model re-fitted without spatial factors to assess their influence. All
205 models included survey method (point or net) and time of day (a.m. or p.m.) as covariates for
206 the probability of detection. Although some stations were surveyed up to 21 times, 99% of all
207 stations were surveyed 12 times or less. To improve the efficiency of model fitting and reduce
208 the computational resources required to run them, we fitted the modes using a maximum of
209 12 replicates per station.

210 Models were fitted using the Bayesian occupancy model package, "spOccupancy" (61). The
211 "spOccupancy" package enables the modelling of all species simultaneously, and accounts for
212 autocorrelation between species. In addition, spatial latent factors, which are akin to
213 unmeasured site-specific covariates that decay with distance, help account for residual
214 species correlations. Fewer factors were favoured to explain variation efficiently and avoid
215 overfitting, particularly with relatively few replicate surveys and rarely detected species. We
216 included three independent spatial factors, each derived from residual species correlations
217 after controlling for other variables and previous spatial factors. Each factor provides a decay
218 rate (phi), with the non-autocorrelation distance calculated as 3/phi.

219 Models were fitted with 50,000 iterations, discarding the first 25,000 as burn-in, and thinning
220 the rest by 50 to produce 500 posterior samples. Each posterior sample provides a probability
221 of occurrence (psi) for each species at each station and a latent presence/absence (z = 1/0)
222 calculated from this probability. Additionally, detection probability (p), given presence, is
223 provided per species per station for a single survey. As spatial models have poor chain
224 convergence, a single chain was used, with mixing assessed visually and via the Geweke
225 diagnostic (62). Models assumed no false presences and treated the entire study as a single

closed season. Model goodness-of-fit was measured using posterior predictive checks to calculate a Bayesian p-value, based on the differences between chi-squared values of observed and predicted data per species, grouped across stations. All models had Bayesian p-values between 0.467 and 0.477, indicating a good fit (63,64), and models were therefore subsequently compared using the widely applicable information criterion (WAIC) (Watanabe, 2010) and metrics of predictive performance. Performance was evaluated at the species-level, using area under the receiver operating curve (AUC), and at the station community-level, using species accumulation and Bray-Curtis's dissimilarity of community composition.

Although model performance differs between training and withheld data, evaluation on independent datasets is rarely undertaken for occupancy models (66). We did so here by withholding a validation dataset comprising two stations per field centre, each surveyed at least three times, totalling 5% of the data. To validate model performance, we incorporated both occurrence and detection probabilities when comparing predictions with observations. Each of the model's posterior samples predicts two occupancy values per species. First is the occupancy probability (psi) per species per site, from which a latent occupancy (z = 1/0) is drawn. Detection probability (p) per species and site in a single survey was predicted, and this remained constant across posterior samples. Total detection probability per species and station was calculated as $1 – (1 – p)^n$, where n is the number of replicate surveys performed. This detection probability generated a binomial detection/non-detection (1/0) event per species per station. Latent detection values were then multiplied by occurrence (psi) and latent occupancy (z) for each species and station per posterior sample. Thus, model performance was based on the predicted probability of detection rather than occurrence in the validation data.

4 Results

4.1 Model fit

All models had Bayesian p-values between 0.467-0.477, indicating a good fit to the data. The model with the lowest WAIC value, thus indicating it was the best-performing model, was fitted with RS reflectance data and included spatial factors, followed by the covariate-free intercept model, the RS reflectance model fitted without spatial factors, and the highest WAIC indicating the worst performance was from the model fitted with environmental descriptors. The probability of detection (*p*) was consistent across all models. Surveys conducted in the morning using net counts had a median species-level p = 0.022, 95% CI [0.001, 0.179]. When conducting surveys in the afternoon, median detection probability significantly lower at p = 0.015, 95% CI [0.001, 0.018]. When using point rather than net surveys, the median p increased significantly to 0.065, 95% CI [0.000, 0.389]. However, point surveys did not significantly increase detection for three of the nine Orders represented. Those three were Caprimulgiformes (nightjars), and Coraciiformes (kingfishers and hornbills), and Galliformes (ground dwelling birds).

The mean probability of occurrence across all species in primary forest and an agricultural habitat, was 0.291, 95% CI [0.211, 0.375]. In secondary forest, the mean occupancy was higher than in primary forest, rising to 0.47, 95% CI [0.36, 0.61]. In comparison to agricultural landscapes, mean occupancy in floodplain increased to 0.36, 95% CI [0.30, 0.47], and in terra-firma mean occupancy increased to 0.37, 95% CI [0.30, 0.47]. Mean occupancy was not shown to vary significantly with deforestation within a 1-2 km radius, but increased by 0.057, 95% CI [0.008, 0.108] with each 10% increase in deforestation within a 5km radius.

When using RS data, the model suggested that spatial autocorrelation extended to 5km, 95% CI [3.3km, 7.5km] for one factor and 7.5km, 95% CI [4.3km, 15km] for each of the other two factors. When using habitat data, the model suggested that spatial autocorrelation extended to 2km, 95% CI [2km, 2.3km] for one factor, to 30km, 95% CI [3.75km, ∞] for another, and the third factor was not significant. These factors represent unmeasured variables that influence the occurrence of species, and fade with distance. Although we do not know what is driving this spatial structure, it can be influenced by anything from local vegetation cover to regional climate or land use. Significant spatial autocorrelation confirm that patterns exist beyond those explained by the known environmental variables.

4.2 Model validation

The predictive performances of models followed the implications made by their WAIC values, and the model that produced the best predictive results was also fitted with RS reflectance data and included spatial factors. When assessed on training data, this model had a mean AUC of 0.88 (SD=0.06) and when predicting to independent validation sites, had a mean AUC of 0.68 (SD=0.18). Species for which predictive performance was considered good (AUC>0.7) (67) are hereafter referred to as high-AUC species, and this model had 49 high-AUC species, the highest of any model. The performance of all four models is shown in Table 1. Species taxonomic order was not shown to have any correlation with its AUC.

The predicted species richness of survey stations (6.86 ± 5.1) was close to the observed average richness (6.00 ± 3.6), but when extended to the entire training dataset the model predictions suggested that it would take much longer to detect the total number of species included (Figure 4(A)). The mean predicted richness of test stations (9.94 ± 3.8) was also

comparable to the observed mean richness (10.82 ± 5.3) and indicated a similar accumulation of species, both across stations (Figure 4(B)), and with increasing replication within a station (Figure 4(C)). The species accumulation curve in Figure 4(C) come from one station that was surveyed 12 times and illustrates the extent to which observed accumulated richness greatly underestimates the total richness expected to be present at each location. A consequence of this was that only a fraction of the species that occur at a station were observed, and therefore the average Bray-Curtis dissimilarity between the list of birds observed and those predicted was 0.8 (± 0.1). In locations with higher observed richness, the surveyed total represented a greater proportion of the true expected total, and the dissimilarity between predicted and observed communities was substantially lower (Figure 5).

4.3 Power to detect change

As a result of low detection probabilities and low mean replicate surveys, it was ascertained that there is a mean probability across all species of 0.20 (±0.24 SD) of detecting a 50% reduction in occupancy in a subsequent survey. There is a 70% or greater probability of detecting a 50% reduction in only five of the 135 species modelled. Thus, if the desire is to determine where occupancies are changing by surveying the same area in the future, the current data cannot provide robust evidence.

Figure 6 illustrates how different numbers of survey stations and replicates per station affect the median power to observe a reduction in bird occupancy. Each panel represents a different proportional change that is sought to be detected, and each y-axis represents the probability of detecting that change in at least half the bird species. The x-axis is the total number of

individual surveys that a study is able to undertake (i.e. one replicate at one station is one survey). Each line represents a different number of sites that the total number of surveys are divided among. For every probability of detecting the panel's proportional change (y-axis), the farthest left line represents the fewest total surveys required, and the most efficient number of sites to survey. For example, if our aims were to have a 70% confidence (0.7 on the y-axis) that we could detect when the occupancy of at least half the bird species had declined by 50% (panel C), the chart suggests that the fewest surveys required would be ~10,000 and spread between 100 and 500 sites. Calculations suggest that the requirements would be three replicate surveys at nearly 50,000 stations, or, if all stations were surveyed 27 times, only 447 stations would be required.

5 Discussion

Using over 3,000 bird surveys conducted in south-eastern Peru, we show that remotely sensed satellite data can slightly outperform landcover models in predicting bird community composition. We also highlight the low detectability of many species, which complicates biodiversity monitoring in rainforests. Although the survey design provided valuable insights into bird communities, it was not optimised to detect temporal change. Our results can guide more efficient survey strategies, leading to enhanced species detection, better capturing community composition, and strengthening the performance of RS models in predicting bird communities across landscapes.

339 ## 5.1 Land class and surface reflectance

340 Studies differ on how forest and farmland affect bird species richness (68,69). We found more
341 species in both floodplain and terra firma forests than in agricultural land, partially aligning
342 with evidence that species richness can increase at forest boundaries, particularly where
343 edges are sharp, such as where forest and agricultural land meet (70,71). Furthermore, the
344 greater stratification and canopy complexity often found in primary forests typically support
345 more specialist, range restricted, and endemic bird species compared to secondary forests
346 (72–74). However, our analysis suggested that secondary forest had a greater species
347 richness, consistent with findings that generalist and disturbance tolerant species as well as
348 species that thrive in more open canopy environments are drawn to those areas, especially
349 when they are connected to primary forest, thereby increasing species richness (75). Greater
350 visibility, vocalisation and bird density in open secondary forests may also lead to more
351 detections (76–78). The low mean number of replicates in our study could make secondary
352 forests appear richer in species than primary forests, due to improved visibility rather than
353 true richness.

354 Secondary forests require the initial loss of primary forests, and localised deforestation can
355 increase bird species richness. Moderate primary deforestation can increase richness of
356 neighbouring forest as displaced individuals move into it (79). It can also increase habitat
357 heterogeneity, promoting colonisation by generalists and disturbance-tolerant species in the
358 deforested area (79). Our findings that deforestation within a 5km radius increased mean
359 occupancy support this. At this scale species dispersal, habitat connectivity, and edge effects
360 shape community composition (80,81). In contrast, no effects were found at smaller
361 distances, suggesting insufficient heterogeneity at that range. We defined deforestation as
362 loss of primary forest, but deforested areas may have regrown into secondary forest, which

363 also showed high species richness. Misclassification could arise from pre-2000 deforestation
364 or from the omission of water bodies from analysis. Within floodplain forests, water levels
365 can fluctuate seasonally (82) and edge effects may occur at interfaces between large water
366 bodies and forests (83). These classification limitations should be considered when
367 interpreting differences in species occupancy across forest types. bird detectability may have
368 varied due to seasonal fluctuations, which are most pronounced in forest fragments and
369 secondary forest (72,84,85). Surveys were performed by multiple observers with varying
370 levels of experience, which can significantly influence bird species detectability (86).
371 Consequently, some variation in detection probabilities may be attributed to differences in
372 surveyor rather than actual ecological differences.
373 Surface reflectance diversity has been used to predict tropical forest and bird diversity (87)
374 and bird species richness found within them (88) and our findings support this. RS data
375 performed as well as, if not better than, land class in predicting bird communities (89,90).
376 Image seasonality and resolution matter for modelling bird communities in temperate regions
377 (89,90). However, persistent cloud cover in our study area required annual composites, and
378 mean reflectance values calculated over thousands of square metres make finer resolution
379 imagery unlikely to improve results.
380 Despite these challenges, our study has shown that RS data have the capacity to improve on
381 land class in predicting bird communities in tropical forests. Two broad land-class groups
382 could be differentiated by plotting the first two PCAs: secondary forest/agriculture and
383 primary forest/terra-firma/floodplain. Within those two groups, secondary forest, defined as
384 land deforested since 2000, had a large overlap with agricultural land, suggesting that
385 deforested land here tends to become agricultural rather than regenerating into secondary
386 forest (91,92). In the other group, primary forest overlapped more with terra-firma and

387 floodplain than with agriculture, though sizeable overlaps between all groups existed. This
388 may be explained by discrepancies brought about by course scale, out of date information or
389 human error in habitat classification (93–95). Additionally, land classes may oversimplify or
390 fail to capture the finer scale variation seen by RS data. Localised secondary descriptors of
391 structural variation, such as deadwood volume and tree girth, can also influence reflectance
392 values, and when included in conjunction with broad habitat type, have been shown to define
393 species richness far better than habitat type alone (96). This shows that RS data better capture
394 gradual changes in vegetation structure than can predefined classes. The challenge for future
395 research will be in deriving RS variables that can describe more ecologically meaningful
396 variation and differentiate between less obvious variations in surface structure.
397

398 ## 5.2 Realities and practicalities of observing change

399 Whether using habitat or RS variables, model success depends on the quality and quantity of
400 the data with which they are trained (97,98). Low detection probabilities suggest substantial
401 effort is needed to detect most species, raising concerns about data sufficiency. However, of
402 the approximately 760 bird species thought to occur in the Tambopata area (99), our study
403 recorded nearly half. This, in terms of both number and proportion of species identified, aligns
404 with findings from other surveys in tropical forests (100–102). Low detection rates likely
405 caused individual surveys to underestimate community composition, making landscape-wide
406 communities appear more distinct than limited survey observations suggest. Nevertheless,
407 the species modelled exhibited patterns of grouping based on both forest habitat descriptors
408 and RS variables, suggesting that they represented more than just random observations. This

409 indicates that, despite describing approximately a half of the full community, our results were
410 reliable.
411 Increased sampling effort revealed more of the local community and improved similarity
412 between predicted and observed communities. Thus, improving detection rates is essential
413 to increasing the proportion of the community observed and improving the predictive output
414 of models. Increasing cumulative detection rates to 80% has been shown to negate the
415 importance of detection on model performance (103). Yet we have shown that it would
416 require a huge effort to reliably observe changes in occupancy for many species. Thus,
417 efficient and accurate surveys are critical to provide high quality data on which to train RS
418 models, especially as ongoing surveys are needed to monitor the effects of conservation
419 efforts on habitat change over space or time. The type of survey conducted affects detection
420 rate, and we agree with Mulvaney & Cherry, (2020) that point counts increase mean detection
421 over net counts. However, these findings are not universal, as it has been shown that within
422 tropical forests, the most effective survey method varies with ecosystem, such as whether
423 the study is within lowland or cloud forest (101). Similarly, transect counts and canopy counts
424 add further depth to the proportions of small-bodied species, canopy and mid-storey species
425 that are detected (86,102). Due to the relatively low community overlap observed between
426 methods found in our study, and aligning with other studies, we would suggest that the use
427 of multiple methods is necessary to improve overall diversity assessment (86,101,102).
428 Further to the survey methodology lies the challenge of recruiting appropriately trained
429 surveyors who are familiar with the bird species of the area, which is a necessity in conducting
430 effective surveys in complex and rich ecosystems such as tropical forests (86). Our results
431 suggest that to effectively detect changes in community composition, it is necessary to
432 perform far more replicate surveys than were performed (86).

5.3 Future potential

Forest degradation in Peru has been shown to increase the amount of carbon released into the atmosphere by almost 50% (105). Protecting forests and carbon sinks has understandably been central of tropical conservation, and government policies and voluntary carbon offset conservation efforts such as REDD+ have successfully slowed the rate of deforestation in recent years and have played a role in mitigating climate change (106). To ensure that the implementation of carbon conservation efforts, such as REDD+, also have a positive impact on biodiversity, ecological monitoring of forests should be aligned with the conservation objectives of the area (107). While REDD+ has had some success in protecting forests globally, the level of success in the Amazon may be overstated due to the overestimation of baseline deforestation (108), highlighting the need to validate the costs of voluntary carbon offset credits. Degradation impacts are not fixed and can be improved by restoration or worsened by repetition and should be measured at a landscape rather than patch scale (109). Measuring community diversity at landscape scales may require impractical levels of monitoring, but patch scale changes in habitat should in principle be observable by Earth observation. Should sufficient, consistent, reliably representative biodiversity data be available to calibrate models fitted with RS data, biodiversity responses to changing land use can be identified. Policy and management should judge the results of practices at the point of implementation rather than judge the practices conceptually as a whole, and by mapping species diversity in conjunction with other measures of landscape health, trends in forest degradation and regeneration over time can be identified (109).

455 Despite the challenges posed by generally low detection rates, our study demonstrated that
456 the occupancy of a third of the bird species with sufficient detections in the Peruvian Amazon
457 can be predicted with reasonable confidence. However, low detection rates limit model
458 capacity to detect community change over time. While RS models may not yet be sufficiently
459 robust for ongoing monitoring, reporting and verification, there is no evidence that field-
460 based methods alone will be able to do this at the scale required. While surveys can identify
461 spatial variations, detecting temporal change requires detailed count data at a level that may
462 be impractical (110). Our power analysis revealed that with the current monitoring structure,
463 even if a species population were to half, we would fail to detect this four out of five times.
464 The suggestion that declines of many species may be substantial before being reliably
465 detected has major implications for conservation monitoring using existing survey design.
466 Improving detection rates will increase the power of future surveys to detect change. Given
467 that resources are limited, future surveys should focus on fewer locations, prioritised across
468 an ecological gradient of interest, with a higher number of replicates; results suggest at least
469 20 per site. This is particularly critical as even basic inventories of avian diversity across much
470 of the tropics are lacking (86). Establishing baseline datasets is essential for enabling future
471 repeat surveys, which could provide valuable insights into how and where tropical bird
472 communities are changing (111). Building on the findings of this study by refining survey
473 design and aligning research with specific conservation objectives will be key to improving
474 biodiversity monitoring in the region so that decisions are based on detectable trends rather
475 than snapshots of biodiversity (112).
476

Declarations

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This study received no specific funding. The bird data used were collected independently by co-authors C.A.K. and C.K. as part of ongoing monitoring activities not funded by the lead or senior authors of this manuscript.

Ethics Statement:

The bird occurrence data used in this study were collected independently by co-authors C.A.K. and C.K. as part of long-term monitoring within the Tambopata National Reserve, Peru. Data collection was conducted ethically and in accordance with local research regulations.

Data Availability:

The data that support the findings of this study are available from the authors upon reasonable request.

Authors' Contributions:

Author contributions: A.C.S., A.B. and I.R.H. conceptualised the study; C.A.K and C.K. performed independent field surveys and provided bird sighting data; A.C.S. sourced and calculated all remotely sensed variables, performed all modelling and analysed results; A.C.S. wrote the manuscript with reviews and edits suggested by A.B, I.R.H.

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Table 1: The fit and predictive performance of the four models analysed. Low WAIC values and high AUC values represent better performances. It can be seen that the best performing model in all categories is fitted with RS reflectance data and includes spatial factors.

Model Covariates	Spatial Factor Included	WAIC value	Delta WAIC	Mean Explanatory AUC	Mean Predictive AUC	Number of high-AUC species
RS Reflectance	yes	66773	0	0.88	0.68	49
RS Reflectance	no	68620	1847	0.87	0.62	31
Habitat Descriptors	yes	69432	2659	0.87	0.58	21
None	yes	66995	222	0.8	0.66	43

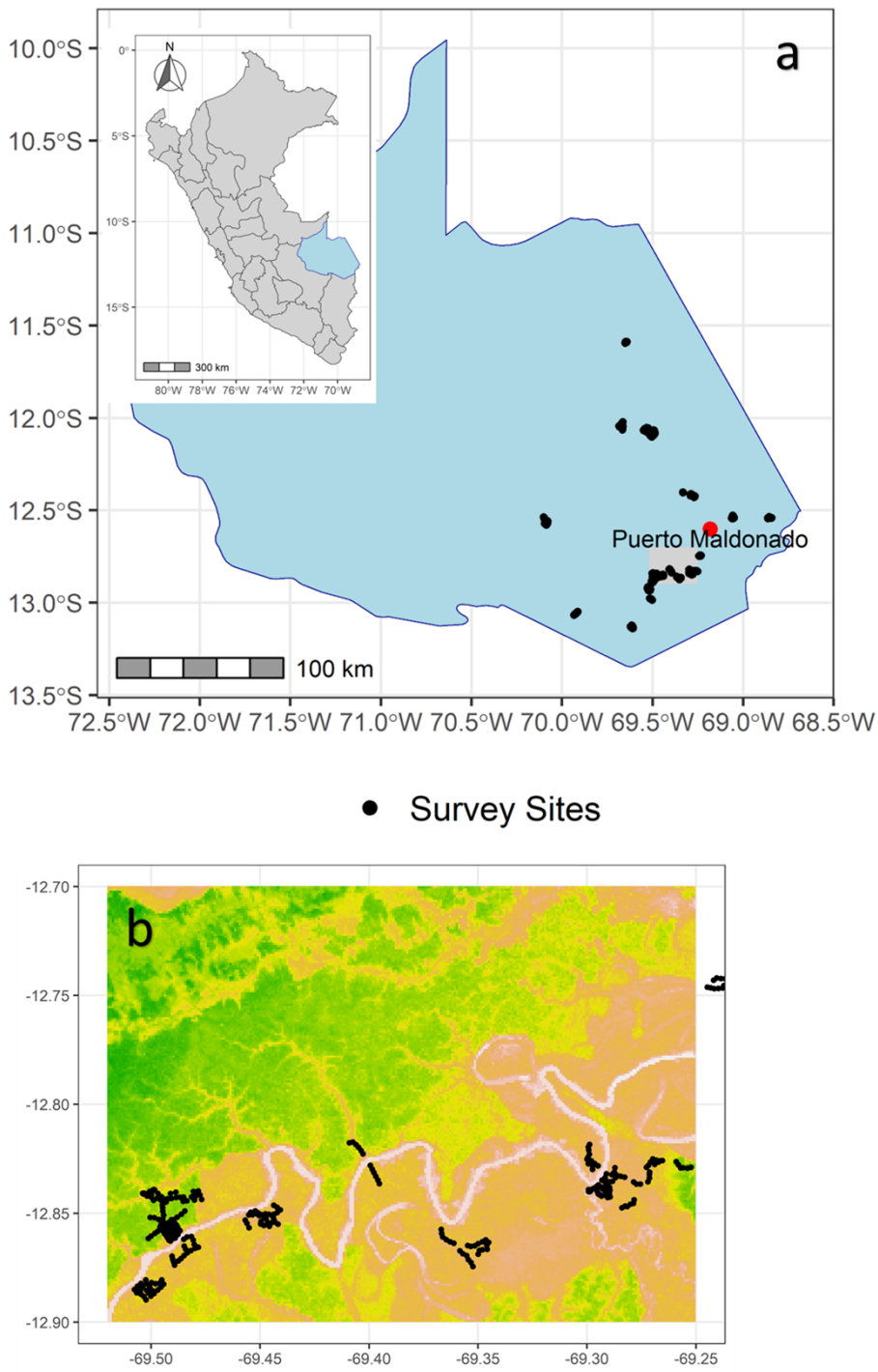

Figure 1: (a) The location of survey stations within the Madre de Dios region. Inset is Peru with Madre de Dios highlighted in blue. Panel (b) displays the distribution of survey stations within the grey box highlighted in panel (a) along the Tambopata River within regional topography (113).

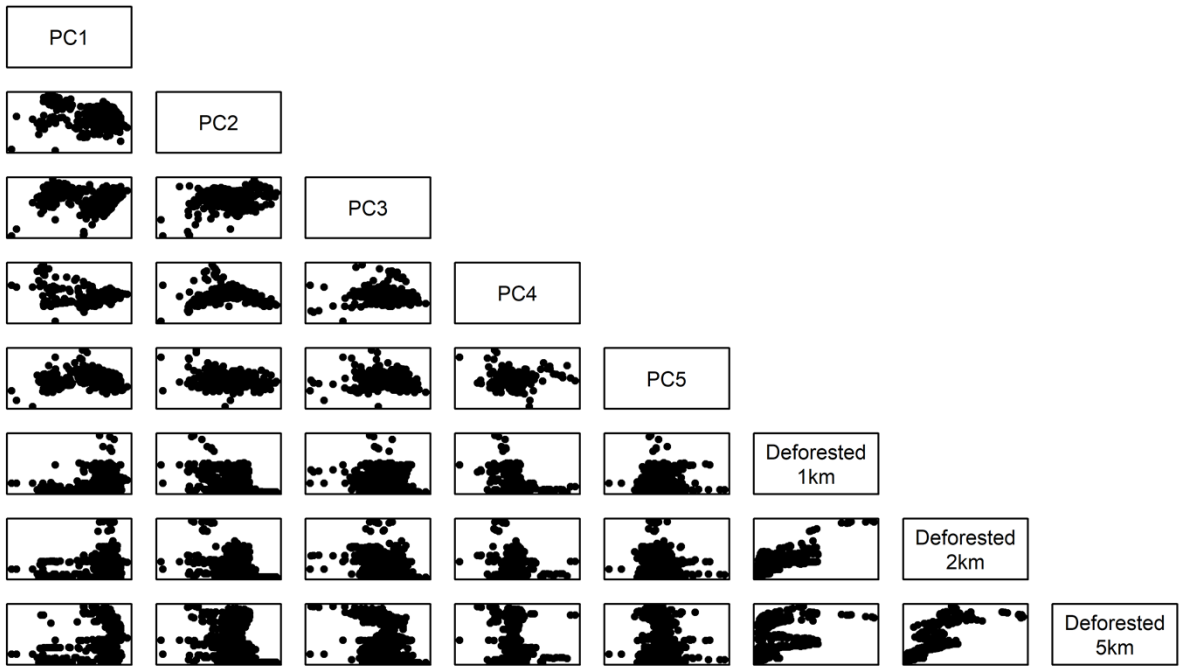

Figure 2: The distribution of variables used in EO models, comprising the five EO derived principal components, and the proportion of deforestation calculated at the three measured areas.

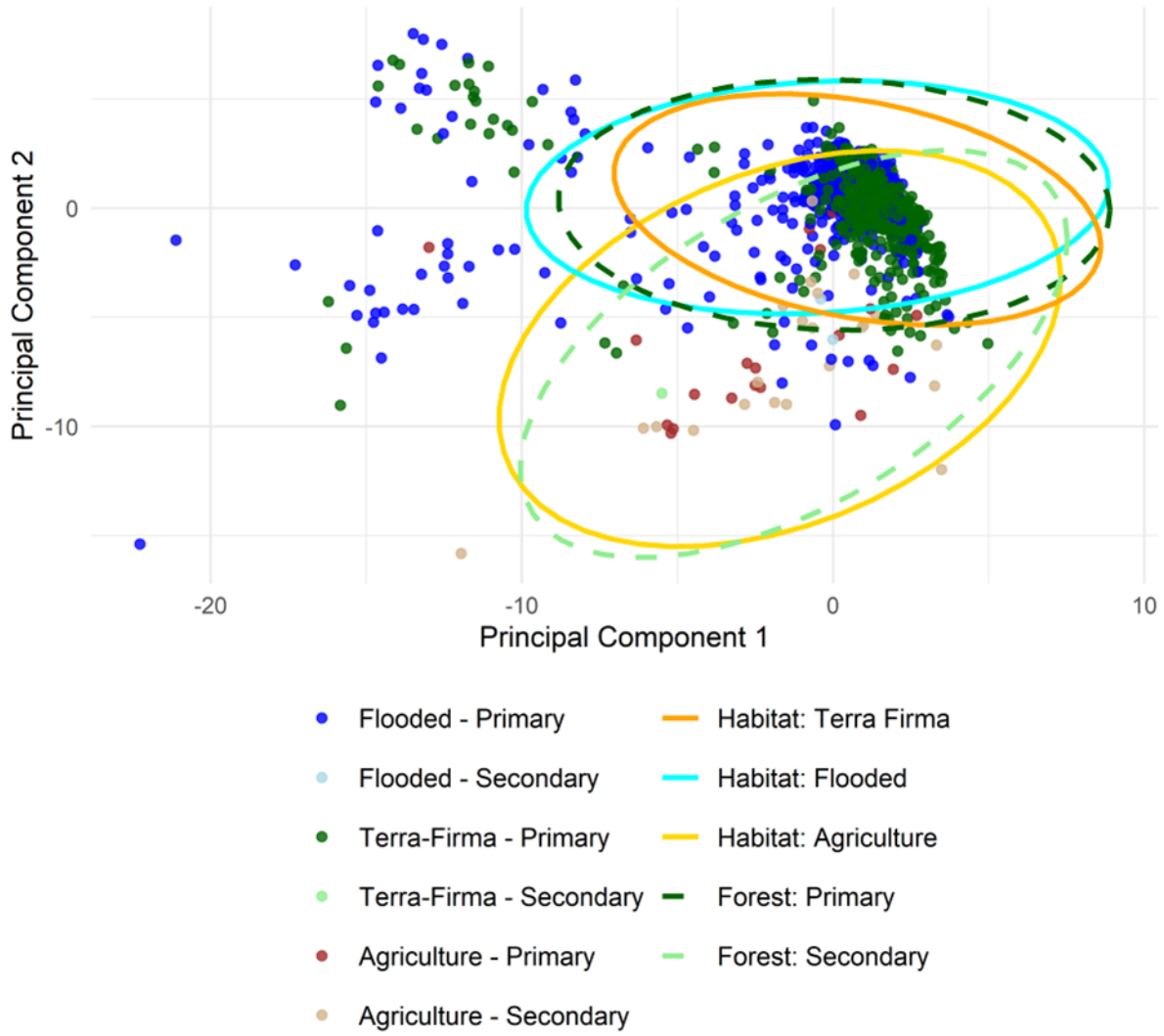

Figure 3: The first two principal components, representing 76% of the variation in the RS data, plotted against each other and showing their relationship with the measured habitat types. Each point represents an individual survey and is coloured based on the combination of habitat (floodplain forest, terra-firma forest, agriculture) and forest type (primary or secondary). Ellipses represent the 95% confidence interval around the mean for each categorical group.

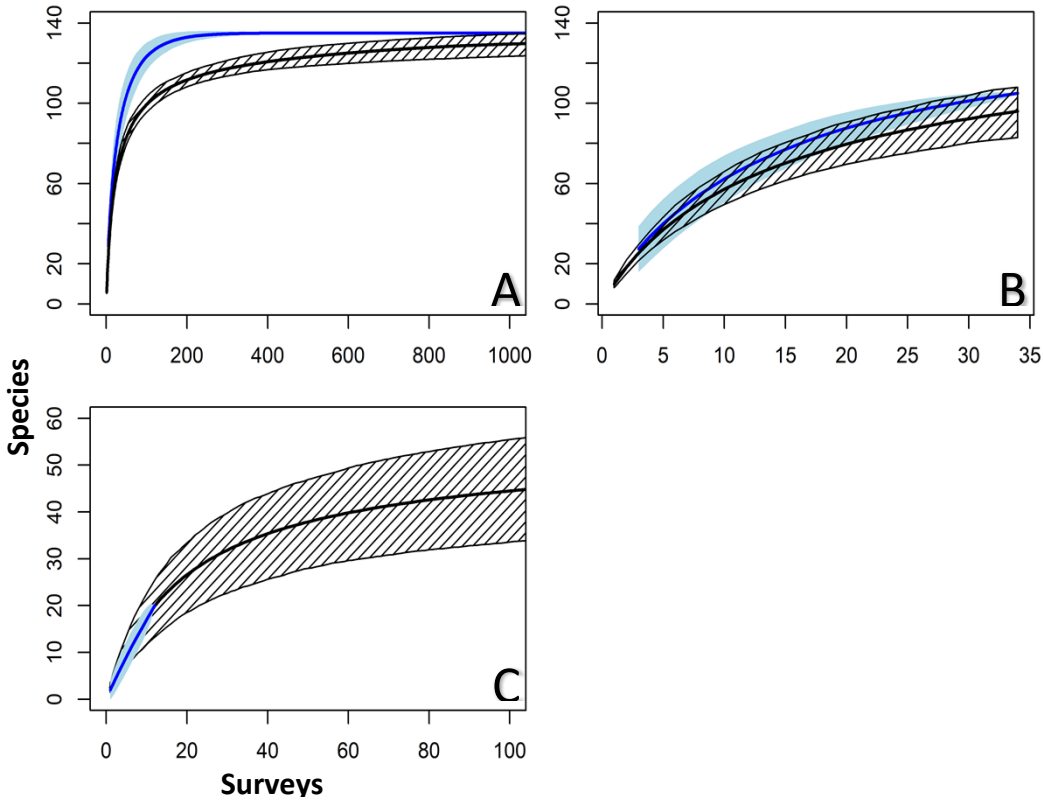

Figure 4: Observed (blue) and modelled (black) species accumulation (±2SD) with increasing numbers of surveyed stations, (A) within the training data, (B) set aside for validation, and (C) based on an increasing number of replicate surveys conducted at a single survey station.

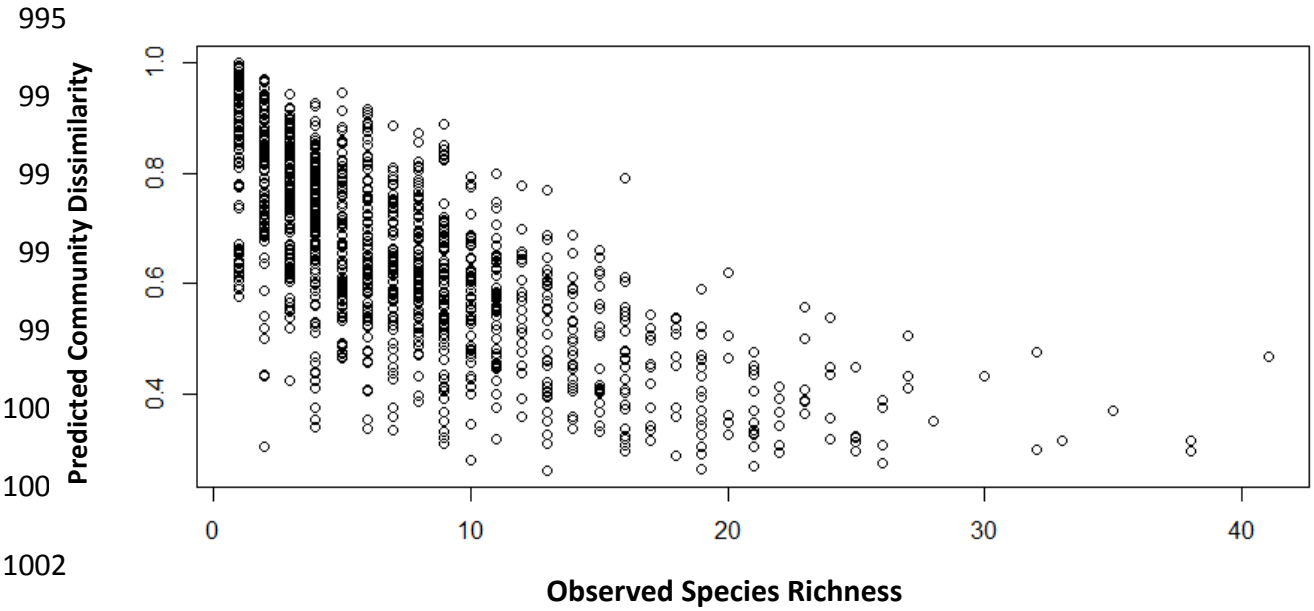

Figure 5: Each point represents a survey station. For each station, modelled dissimilarity is the mean dissimilarity between each of the communities produced by the model's 500 posterior samples, and the observed community.

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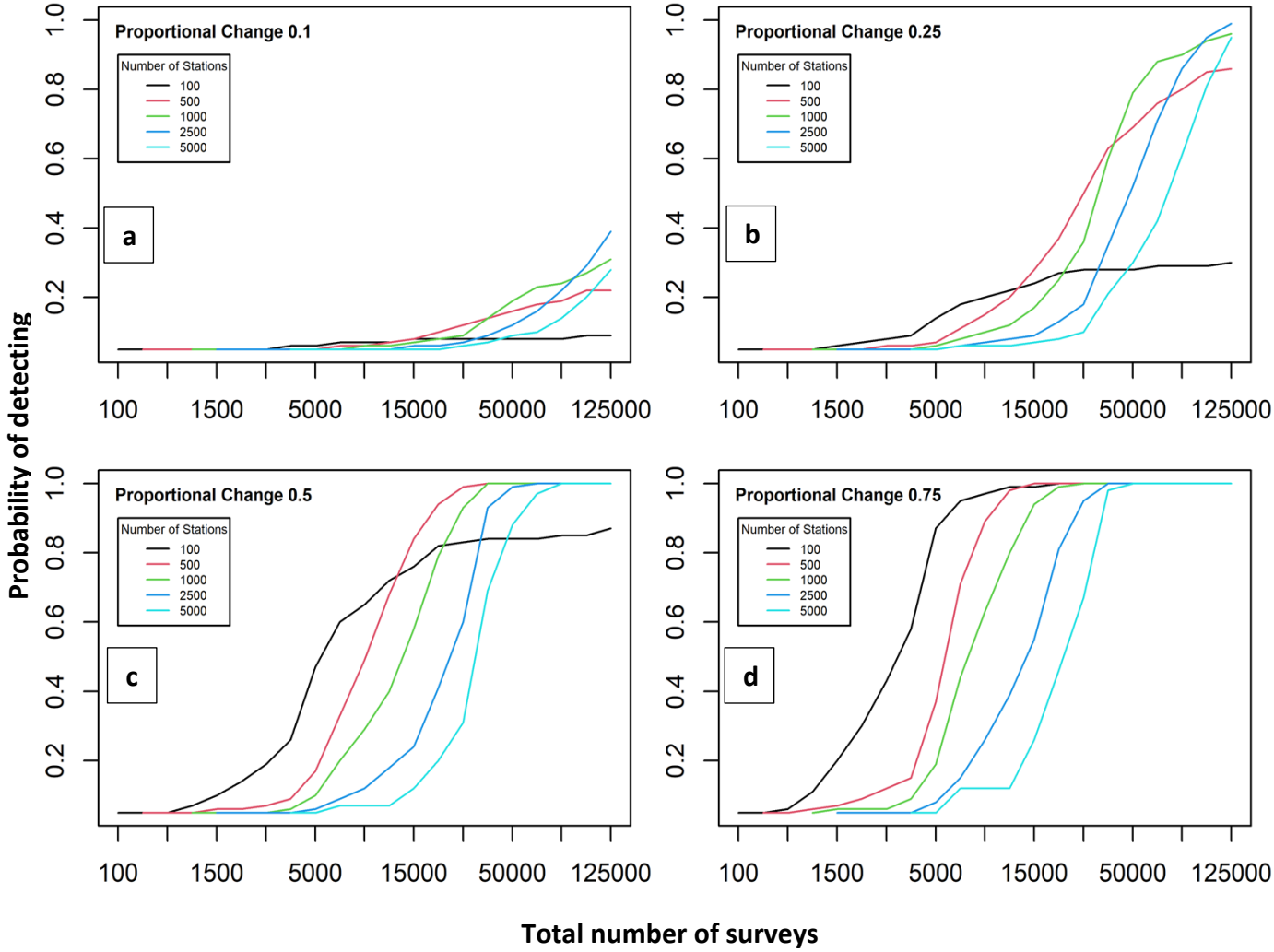

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1009 Figure 6: The influence of survey effort on the probability of detecting a reduction in occupancy in

1010 future surveys. Survey effort was calculated as the number of stations surveyed * number of replicate

1011 surveys per station. Each line represents a different number of stations and was calculated as the

1012 mean value across all 135 species modelled. Each chart represents a different proportional reduction

1013 in occupancy.