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Imperfect detection biases β diversity estimates based on whether species are shared between sites

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ABSTRACT

Imperfect detection is a form of sampling error that can bias measurements of species occurrence and is widely known to bias measures of local (α) and regional (γ) diversity. However, it is less well known how imperfect detection affects estimates of β diversity, the variation in species composition among sites, especially when incorporating species traits and evolutionary histories. Using a decade of avian monitoring data collected across 36 subtropical islands, occupancy model was applied to correct imperfect detection and to quantify its impact on taxonomic, functional, and phylogenetic β diversity in relation to island area and isolation. To assess the broader generality of these patterns, simulations were conducted incorporating multiple ecological and sampling drivers, including survey design and community structure. Both empirical and simulated analyses revealed that imperfect detection consistently led to overestimates of taxonomic, functional, and phylogenetic β diversity, primarily due to the under-detection of shared species, which, in turn, obscured diversity relationships with island attributes. In the empirical dataset, the extent of overestimation increased with greater differences in island area, whereas simulations demonstrated that repeated surveys per site effectively reduced this bias. Collectively, these findings establish a general framework explaining how imperfect detection systematically biases all facets of β diversity by altering observed species composition. This mechanism offers broad applicability across various biological taxa and ecological systems, enhancing the accuracy of biodiversity measurements, particularly functional and phylogenetic diversity. Given the importance of β diversity in understanding spatial and temporal community turnover, it is imperative to prioritize its accurate quantification.

Keywords: Birds; Functional β diversity; Imperfect detection; Island biogeography; Phylogenetic β diversity; Shared species

INTRODUCTION

Accurate information on species occurrence underpins biodiversity research, forming the basis for understanding species distributions, community composition, and conservation prioritization (MacKenzie et al., 2002). However, species frequently go undetected during field surveys, resulting in false negatives, collectively referred to as imperfect detection (MacKenzie et al., 2002). Accounting for this detection bias has become integral to modern analytical frameworks used to estimate species richness within a site (α diversity) (Dorazio et al., 2006) or across all sites in a region (γ diversity) (Tingley et al., 2020). When a species present at a site is missed, α diversity is inevitably underestimated (MacKenzie et al., 2006). In contrast, β diversity, which quantifies variation in species composition among sites (MacArthur, 1965; Whittaker, 1960), responds to imperfect detection in more complex ways, as errors in α diversity do not necessarily translate linearly into errors in estimates of β diversity.

Estimating β diversity involves comparing multiple assemblages based on both the number of shared and unique

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species between them (Baselga, 2010). An undetected species in one or more sites can either be shared between paired assemblages or unique to one of the assemblages. When shared species are more likely to go undetected than unique species during field surveys, the total number of species across sites (i.e., α diversity) declines, while the total number of unique species increases proportionally. This distortion inflates dissimilarity estimates, yielding an overestimate of β diversity. In contrast, when unique species are disproportionately missed, the perceived distinctiveness among assemblages diminishes, leading to an underestimation of β diversity. Thus, the influence of imperfect detection on β diversity hinges on whether undetected taxa are shared among sites or restricted to particular sites (Figure 1), emphasizing the need to explicitly account for detectability in comparative biodiversity assessments.

Although the preceding reasoning is framed within a taxonomic context, taxonomic diversity assumes all species are equivalent and disregards their functional attributes and evolutionary histories (Cadotte et al., 2011). Contemporary biodiversity research increasingly integrates multiple dimensions of diversity, including functional and phylogenetic aspects (Cadotte et al., 2019; Devictor et al., 2010). The conceptual foundation of species compositional status—whether species are shared or unique to assemblages—can be extended to these dimensions. Functional and phylogenetic β diversity incorporate ecological differentiation derived from species traits and phylogenetic relationships, both of which can influence detectability (Si et al., 2018). When a species occupying a shared or unique position in functional space or along a phylogenetic branch remains undetected, corresponding measures of functional and phylogenetic β diversity may become overestimated or underestimated, respectively. This study introduces a conceptual framework illustrating how imperfect detection biases β diversity depending on whether undetected species are shared or unique across assemblages and investigates systematic biases in β diversity estimation arising from trait- and lineage-

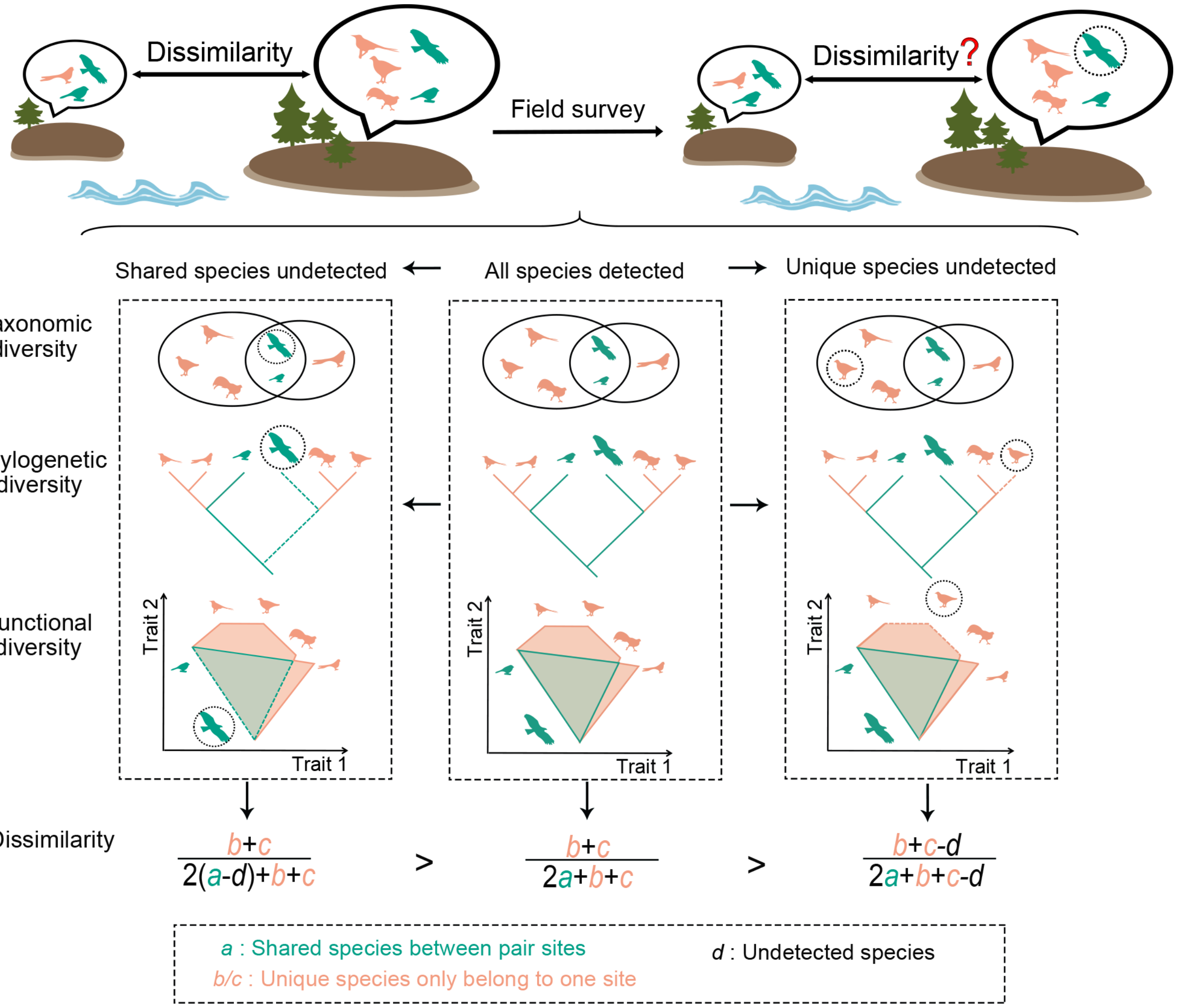

Figure 1 Hypothetical framework describing β diversity estimates in two scenarios under imperfect detection of species using the Sørensen index

Undetected species are either shared species between paired assemblages or unique species only belonging to one assemblage. In the Sørensen index, *a*, *b*, *c*, and *d* represent the number of shared species (green), unique species of one of the paired sites (orange), unique species of another site of the paired sites (orange), and undetected species (dotted circles or lines) during field survey, respectively. Imperfect detection of shared and unique species can overestimate and underestimate estimated dissimilarity (i.e., "true" β diversity), respectively. See Supplementary Appendix S3 for further details.

dependent detectability (Figure 1).

The susceptibility of taxonomic, functional, and phylogenetic β diversity to imperfect detection varies not only in how each measure incorporates species dissimilarity but also in whether the underlying functional or phylogenetic distances are structured or random. To understand how metrics might deviate from one another, it is critical to examine the extent (or magnitude) of biased estimates of β diversity (i.e., the difference of β diversity before and after accounting for imperfect detection; Δβ). Such extent of bias in β diversity estimates may differ among taxonomic, functional, and phylogenetic dimensions. For instance, when numerous shared species go undetected, taxonomic β diversity tends to be overestimated. However, this pattern may differ for functional and phylogenetic β diversity if the undetected shared species possess similar traits or close evolutionary relationships (Si et al., 2018). In such cases, the overestimation of functional and phylogenetic β diversity will remain low, even when taxonomic β diversity is substantially overestimated.

Additionally, taxonomic, functional, and phylogenetic dimensions of β diversity are likely to exhibit varying sensitivity to imperfect detection along environmental gradients. Sites that diverge strongly in environmental characteristics, such as area, canopy cover, elevation, or latitude, often differ in both species detectability (e.g., closed vs. open habitats) and occupancy conditions (e.g., primary vs. marginal habitats) (MacKenzie et al., 2002, 2006). In either case, when detectability or occurrence varies among sites, uncorrected samples affected by imperfect detection will inevitably differ among sites. For example, islands with larger differences in area or isolation are more likely to present contrasting occurrence conditions for shared species. Although such species may generally exhibit higher detectability due to broader ecological plasticity, exposure to heterogeneous conditions across islands increases the likelihood of non-detection at some sites. Consequently, as site pairs diverge along environmental gradients that influence detectability, imperfect detection exerts progressively stronger bias on β diversity estimates.

Over the past decade, approaches for correcting biodiversity estimates for imperfect detection have advanced beyond purely taxonomic perspectives to encompass functional and phylogenetic dimensions, including both non-parametric (Chao et al., 2006, 2014, 2019, 2023) and parametric approaches such as occupancy models (Dorazio et al., 2010; Dorazio & Royle, 2005; Jarzyna & Jetz, 2016). In taxonomic diversity analyses, correcting for detection bias requires estimating only the number of undetected species rather than identifying which specific species were missed. Functional and phylogenetic diversity, however, explicitly depend on species identities because they capture ecological and evolutionary differentiation among taxa. Non-parametric estimators have recently been extended to account for imperfect detection in functional and phylogenetic β diversity through a multiplicative framework (i.e., $\beta=\gamma/\alpha$) derived from Hill numbers (Chao et al., 2023). Nonetheless, these methods treat both detected and undetected species as randomly distributed, potentially misrepresenting true diversity patterns when non-detection is non-random with respect to species traits or phylogenetic relatedness.

Unlike non-parametric estimators, occupancy models explicitly incorporate species identities by hierarchically modeling detection and occupancy probabilities across sites (or sampled locations) (Iknayan et al., 2014; MacKenzie et al., 2006), allowing inference on which species are present but undetected within each community. For α diversity, prior work has demonstrated that accounting for species identity is crucial to mitigating biases in functional and phylogenetic diversity estimates arising from imperfect detection (Jarzyna & Jetz, 2016). Occupancy models therefore provide a powerful framework not only for quantifying *how many* species remain undetected in a community but also for identifying *which* species (and consequently their respective traits and lineages) are missing from observed assemblages. Empirical applications of occupancy models in the context of β diversity have primarily focused on taxonomic turnover across long-time spans (Tingley & Beissinger, 2013) or among habitats with contrasting detection conditions (Tingley et al., 2016). However, few studies have explored the extent of bias in β diversity estimates along environmental gradients or how such bias differentially impacts functional and phylogenetic estimates of β diversity.

This study applied a decade-long detection-non-detection dataset of avian surveys conducted across 36 reservoir islands in Thousand Island Lake, China, encompassing broad variation in island area and isolation, to evaluate the proposed framework. Multi-species occupancy models were employed to correct for species detectability when estimating taxonomic, functional, and phylogenetic β diversity. To assess the generality of the observed patterns, three sets of simulations were developed incorporating a range of ecological and methodological drivers related to sampling design, study design, and community structure, thereby quantifying the extent of bias in each β diversity dimension. Using both empirical and simulated approaches, this study addressed two key questions: (a) how imperfect detection influences estimates of avian taxonomic, functional, and phylogenetic β diversity, and (b) how the extent of these biases varies along environmental gradients, such as differences in area and isolation.

MATERIALS AND METHODS

Empirical evaluations

Study area and islands: The study was conducted in Thousand Island Lake, China (N29°22′–N29°50′, E118°34′–E119°15′), a reservoir land-bridge island system created in 1959 following the completion of the Xin'anjiang Dam. The inundation produced a 580 km^2 waterbody containing 1 078 islands of varying sizes, generating a highly fragmented landscape. The region experiences a typical subtropical monsoon climate, and island vegetation is dominated by secondary successional forest primarily composed of *Pinus massoniana* (Si et al., 2024).

In total, 36 islands were selected to represent a broad gradient of area and isolation, two central determinants in island biogeography (MacArthur & Wilson, 1967). Island areas ranged from 0.57 ha to 1 289.23 ha, while isolation, measured as the shortest distance from the focal island to the nearest mainland, spanned 21.85 m to 3 712.31 m (Supplementary Figure S1).

Sampling methods: Bird communities were surveyed along 53 line transects following standardized protocols (Bibby et al., 2000). Transects were established using stratified random placement to ensure representation of all habitat types within each island (Si et al., 2014). Total transect length (i.e., sampling effort) per island was roughly proportional to the logarithm of island area to account for increasing habitat heterogeneity with increasing island area (Schoereder et al., 2004). Accordingly, eight transects were established on the largest island (island B1; area>1 000 ha) (Supplementary Figure S1), four on each of two islands between 100 and 1 000 ha, two on each of four islands between 10 and 100 ha, and one on each of the remaining 29 small islands (around 1 ha). Individual transects measured 400 m in length, except on islands too small to accommodate that distance. On islands containing multiple transects, a minimum spacing of 500 m was maintained to prevent resampling of individuals (Bibby et al., 2000). Although the number of transects varied with island area, analyses were performed using bird detection-non-detection data at the transect level rather than aggregated by island level, thereby controlling for variation in sampling effort (Si et al., 2018).

Bird data: Bird detection-non-detection data were collected over a 10-year period (2007–2016). Surveys were conducted annually during the breeding season (April–June) using standardized line-transect methods. Surveys were performed only under favorable weather conditions. Morning surveys began 30 min after sunrise and concluded by 1100h, while afternoon surveys were carried out from 1500h and until 30 min before sunset. To ensure consistency among surveys, transects were walked at a uniform speed of approximately 2.0 km/h, with the walking direction assigned randomly for each sampling event. All bird species observed or heard along a transect were recorded. Across the study period, 114 surveys were completed (15 per breeding season during 2007–2010 and nine per season during 2011–2016). In total, 77 terrestrial breeding bird species (hereafter referred to as “birds”) were documented (Si et al., 2018), and their corresponding functional and phylogenetic diversity information was compiled. All diversity metrics, including species richness, functional space, and phylogenetic branch length, followed a Poisson distribution across the 36 islands (Supplementary Figure S2).

Functional trait data were obtained through field measurements and from two key references: *Fauna of Zhejiang: Aves* (Zhuge, 1990) and *The Handbook of the Birds of China* (Zhao, 2001). Traits associated with resource utilization, energetic demand, and trophic position were selected to quantify functional diversity. These included three continuous traits (body mass, body length, and clutch size) and four categorical traits (feeding guild, feeding stratum, feeding behavior, and nest type). Feeding guilds were categorized as carnivore, granivore, insectivore, nectivore, or omnivore; feeding strata as ground, understory, midstory, canopy, or aerial; feeding behaviors as glean, leap, probe, or sally; and nest types as cavity, tree, shrub, or ground (Si et al., 2018).

Phylogenetic relationships among the 77 recorded birds were obtained from *BirdTree* (http://birdtree.org) by pruning the global birds’ phylogenetic tree under the option of “Hackett All Species: a set of 10 000 trees with 9 993 OTUs each” (Jetz et al., 2012). From 5 000 pseudo-posterior distributions, a Maximum Clade Credibility tree with mean node heights was generated using TreeAnnotator v.1.8.2 within the “*BEAST*” package (Drummond & Rambaut, 2007; Si et al., 2018).

Community occupancy model: A multi-species occupancy model (MSOM) without data augmentation (Dorazio et al., 2006) was employed to estimate species occurrence across islands while explicitly accounting for imperfect detection. The model structure followed the framework of Si et al. (2018), with further methodological details and assumptions provided in Supplementary Appendix S1. The analytical framework was based on a single-season occupancy design (MacKenzie et al., 2002), extended to a MSOM using hierarchical normal random effects on all intercepts and slopes (Iknayan et al., 2014). Because all focal species occupied broadly similar island habitats, a single hyper-distribution was specified for each parameter rather than *a priori* species groupings (Ruiz-Gutiérrez et al., 2010). Each year represented the primary sampling period, within which population closure was assumed over the 9–15 repeat surveys conducted annually. Individual transects, rather than entire islands, served as the units of analysis to control for unequal sampling effort across islands. Structural correlation among transects located on the same island was modeled using island-level random effects for occurrence, while temporal autocorrelation in species presence across years was captured through a Markovian autologistic parameter, following the approach of Si et al. (2018).

For the observation process, species detectability (i.e., the probability of detecting species occupied at a given site) was modeled as a function of transect length, survey date (i.e., the ordinal day of year), and categorical time of day (i.e., morning or afternoon). For the ecological process, species occurrence was modeled as a function of island area and isolation. After running the MSOM, an estimated (“true”) occurrence state matrix (“z-matrix”) was obtained, representing the presence-absence states of 77 species across 53 transects over 10 years, each supported by 3 000 Bayesian posterior samples. The MSOM was implemented in R using the “*R2jags*” package.

From the transect-level “z-matrix”, an island-level occurrence matrix was subsequently derived. Of the 36 surveyed islands, seven contained multiple transects, whereas 29 had only one. For each large island, the island-level z-matrix was derived by aggregating species occurrence across all surveyed transects and transforming the counts into a presence-absence matrix. For the 29 smaller islands with only a single transect, the island-level occurrence matrix was identical to the transect-level matrix. In this study, “z-matrix” represented the island-level estimated occurrence state matrix.

Calculating β diversity: Estimated β diversity of bird assemblages was quantified using the “z-matrix”, species trait data, and phylogenetic trees. Taxonomic, functional, and phylogenetic β diversity were measured with the Sørensen dissimilarity index (T_{est}, F_{est}, and P_{est}) implemented in the R package “*betapart*”. Each independent posterior sample of the z-matrix generated corresponding β diversity estimates, yielding 3 000 posterior values per metric. Mean values and 95% Bayesian credible intervals were then derived from these posterior distributions. To enable direct comparison, the observed detection-non-detection matrix was used to calculate observed taxonomic, functional, and phylogenetic β diversity across 630 island pairs (C_{36}^{2}), following identical computational procedures. These observed metrics were assumed to reflect bias arising solely from imperfect detection, with no false-positive records. Comparison of observed and posterior distributions of estimated β diversity allowed assessment of detection bias; observed values falling outside the 95%

Bayesian credible interval of the estimated metrics were interpreted as significantly different.

To evaluate whether imperfect detection bias originated primarily from undetected shared species, correlations between species detectability and the mean probability of being shared among islands were tested using Spearman's rank correlation (Supplementary Appendix S2). Additional analyses examined correlations between detectability and body mass, body length, and phylogenetic position of shared species to identify potential ecological and evolutionary factors influencing detectability (Supplementary Appendix S2).

In this study, the definition of "bias" followed statistical and ecological conventions (Walther & Moore, 2005; Richter et al., 2021; Tingley et al., 2020), where "bias" refers to non-random error, in contrast to "noise", which refers to random error. In this analysis, a consistent tendency for one measure of β diversity to yield higher or lower estimates than another was interpreted as a non-random, directional deviation classified as "bias" rather than "noise". Although such bias may not necessarily alter overarching inferences—for instance, by reversing the direction of an effect (Richter et al., 2021)—a persistent, systematic shift in effect magnitude represents a meaningful form of bias that warrants recognition (Walther and Moore, 2005).

Relationships between β diversity and island gradients: Correlations between β diversity and island attributes were quantified by constructing distance matrices for island area and isolation using the "*dist*" function in the R package "*stats*". Mantel tests were then applied to evaluate correlations between β diversity and these environmental gradients. To determine the influence of imperfect detection on these relationships, mean estimated and observed values of taxonomic, functional, and phylogenetic β diversity, derived from the z-matrix and raw observed-only data, were regressed against differences in island area and isolation using Multiple Regression on distance Matrices (MRM) implemented in the R package "*ecodist*".

The extent of bias in β diversity estimation was quantified as the difference between observed and mean estimated β diversity, expressed as:

$$\Delta\beta = \beta_{\text{obs}} - \beta_{\text{est}} \tag{1}$$

Where β_{obs} is the observed value and β_{est} is the mean estimated value. This metric captured the extent and direction of deviation arising from imperfect detection. Finally, the extent of bias in taxonomic, functional, and phylogenetic β diversity was regressed against the differences in area and isolation using MRM.

Simulations

To assess the generality of the empirical findings and to inform field design for studies of β diversity, three groups of simulations were conducted to evaluate how (i) study design and community characteristics, (ii) species compositional status, and (iii) species traits and phylogenies influence β diversity estimates under imperfect detection. A summary of the simulation framework is provided below, with detailed descriptions available in Supplementary Appendix S3.

In the first set of simulations (i), parameters were varied to examine the effects of survey design and community characteristics. Key variables included the number of survey sites (seven or 36), number of replicate surveys per site (one, three, five, or seven replicates), community size (77 or 150 species), and the mean and variance of occupancy and detection probabilities. These combinations generated communities exhibiting different levels of detection error and occupancy heterogeneity. To limit parameter complexity, seven scenarios of detection-occupancy hyperparameters were selected to reflect both "ideal" and "non-ideal" scenarios (Supplementary Table S1). The ideal scenario assumed high and relatively uniform detection and occupancy probabilities (community type 1), while two non-ideal scenarios represented low mean detection and occupancy probabilities with either high (community type 6) or low (community type 7) interspecific variance (Supplementary Table S1). The remaining four scenarios enabled evaluation of the effect of modifying a single factor—either mean or variance of detection or occupancy probability—relative to the ideal scenario. These scenarios included community with high variation in occupancy probability (community type 2) or detection probability (community type 4), and community with low average occupancy probability (community type 3) or detection probability (community type 5) (Supplementary Table S1).

Across all configurations, 56 000 synthetic datasets were generated, encompassing 112 parameter combinations and 500 replicates per combination. For each dataset, both "true" and "imperfectly-observed" β diversity values were computed using the Sørensen dissimilarity index. The extent of bias in β diversity was determined as a function of (*observed β diversity–true β diversity*)/*true β diversity*) (see Supplementary Appendix S3 for further details), enabling evaluation of how sampling design and community characteristics affected the accuracy of β diversity estimation.

The second simulation (ii) focused on the role of species compositional status (i.e., shared species between two assemblages, or unique species belonging to only one assemblage) on biasing β diversity under imperfect detection. Two scenarios were simulated: imperfectly-observed shared species and imperfectly-observed unique species. The number of shared, unique, and undetected species was randomly drawn from Poisson distributions. For each case, "observed" β diversity values were calculated using modified Sørensen and Jaccard dissimilarity indices and compared with "true" β diversity values derived from complete detection (see Supplementary Appendix S3 for further details).

The third simulation (iii) explored how imperfect detection driven by species traits or phylogenetic relatedness biases β diversity. A metacommunity was simulated using the "*sim.meta.phy.comm*" function in the R package "*pez*" to model different detection scenarios. For phylogenetic effects, two imperfect detection processes were modeled: imperfectly-observed phylogenetically redundant species and imperfectly-observed phylogenetically distinct species. Similarly, for trait-based effects, two scenarios were tested: imperfectly-observed functionally redundant species and distinct species. An undetected scenario based on species compositional status, i.e., shared or unique species, was also run. Seven β diversity metrics were computed: taxonomic, functional, and phylogenetic β diversity, each derived from incidence data using the Sørensen and Jaccard indices, as well as abundance-based taxonomic β diversity calculated using the Bray-Curtis index. These metrics were compared between complete and imperfect detection scenarios to evaluate how undetected traits, lineages, or compositional differences bias estimates of β diversity (see Supplementary Appendix S3 for further details).

Finally, a supplementary simulation was performed using the empirical dataset as the “true” reference to assess how detection bias affects the relationship between β diversity and environmental gradients (i.e., island area and isolation) (Supplementary Appendix S3). Collectively, these simulations highlight the mechanisms by which detection bias distorts β diversity estimation across ecological contexts and provide recommendations for designing robust field surveys and analytical approaches.

RESULTS

Empirical evaluations

Analyses revealed that the non-detection of shared bird species during field surveys led to significant overestimation of functional and phylogenetic β diversity, but not taxonomic β diversity (Figure 2; Supplementary Table S2). Shared species exhibited a higher likelihood of being missed during surveys (Spearman’s ρ=–0.559, P<0.05) (Supplementary Figure S3B and Table S3). The probability of non-detection was associated with species traits, particularly body mass (Spearman’s ρ=–0.263, P<0.05) (Supplementary Figure S4A) and body length (Spearman’s ρ=–0.226, P<0.05) (Supplementary Figure S4B). Comparisons between observed (T_{obs}, F_{obs}, and P_{obs}) and detection-corrected (T_{est}, F_{est}, and P_{est}) β diversity, including their associated uncertainty, showed that T_{obs} did not differ significantly from corrected estimates, as indicated by overlapping 95% credible intervals. In contrast, both F_{obs} and P_{obs} were significantly overestimated relative to their detection-corrected counterparts (Figure 2; Supplementary Table S2). These findings confirm that imperfect detection introduces systematic bias in β diversity estimation and that the extent of this bias varies among taxonomic, functional, and phylogenetic dimensions. The results further support that detection bias is influenced by species traits and evolutionary histories, leading to distinct levels of bias across the three diversity metrics.

Observed functional and phylogenetic β diversity increased significantly with differences in island area (F_{obs}, P<0.05, and P_{obs}, P<0.01), while taxonomic β diversity showed no significant association (T_{obs}, P>0.05; Figure 3; Supplementary Table S4). After accounting for imperfect detection, none of the corrected estimates (T_{est}, F_{est}, and P_{est}) exhibited significant relationships with area differences (P>0.05) (Figure 3; Supplementary Table S4). In contrast, observed

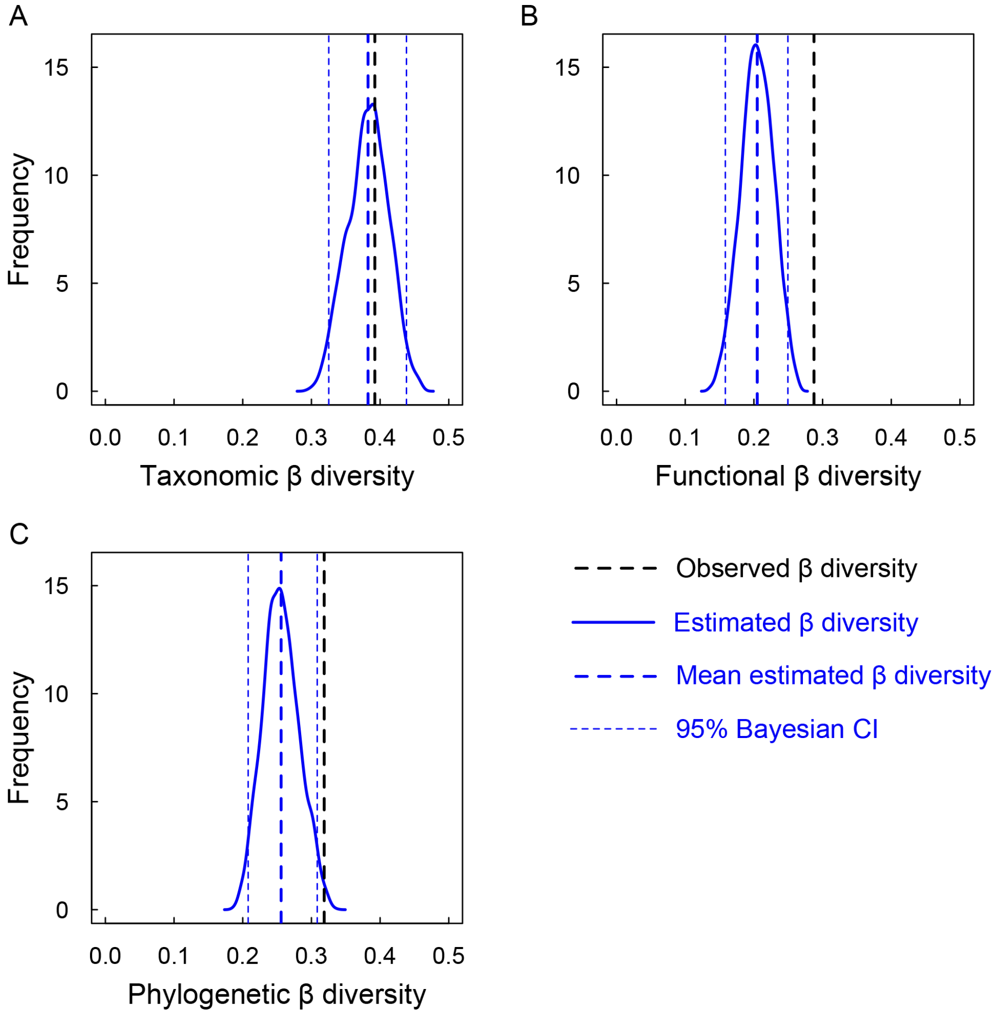

Figure 2 Estimates of β diversity before and after accounting for imperfect detection of breeding birds on 36 islands in Thousand Island Lake, China

A: Taxonomic β diversity. B: Functional β diversity. C: Phylogenetic β diversity. Blue solid line represents posterior distribution of estimated β diversity. Blue and black dashed lines represent mean estimated β diversity and observed β diversity, respectively. Light blue dashed lines represent 95% Bayesian credible intervals of estimated β diversity. See Supplementary Table S2 for related results.

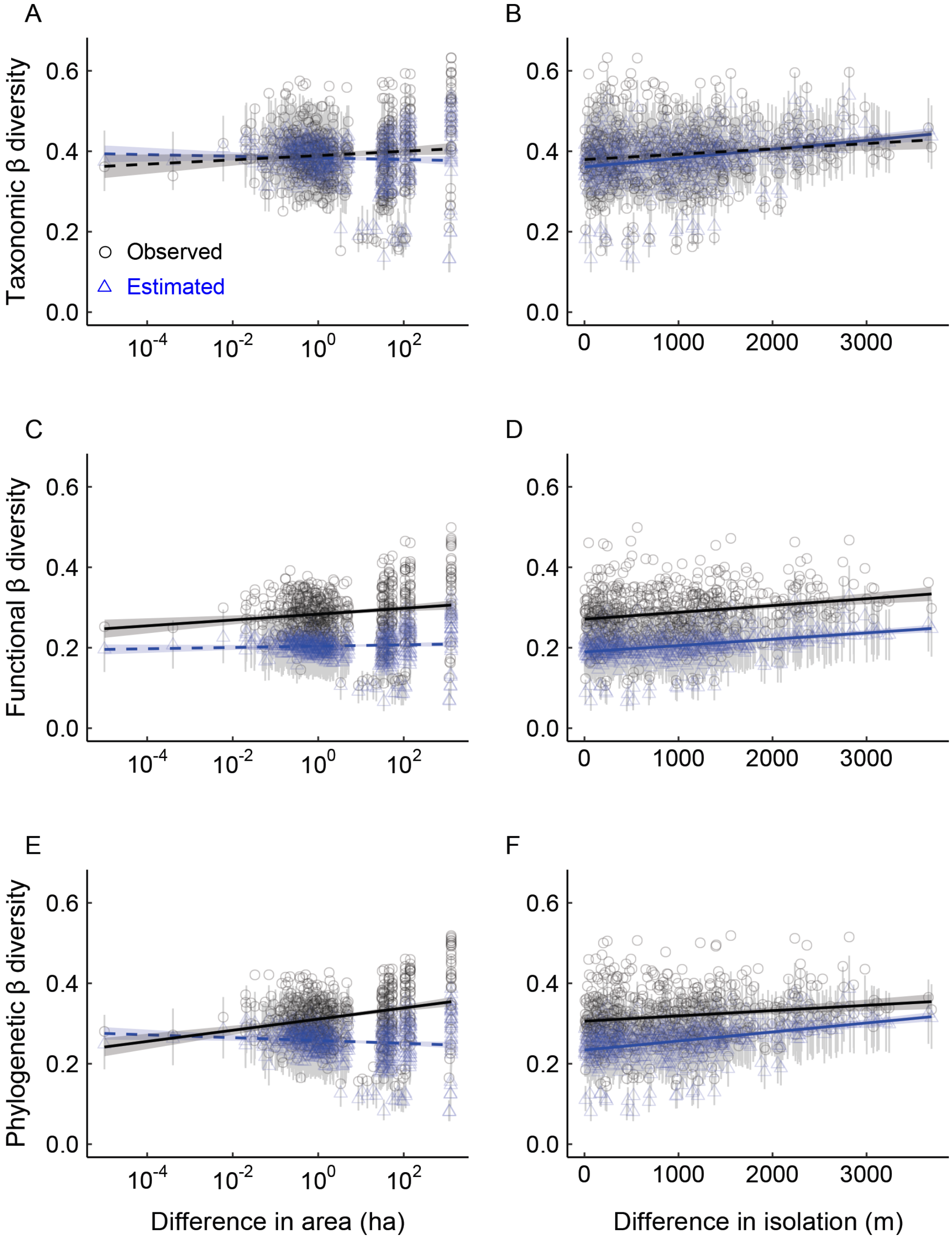

Figure 3 Relationships between β diversity of breeding birds on 36 islands in Thousand Island Lake, China, calculated from observed (black circles) and estimated (blue triangles) occurrence matrices, and differences in area and isolation

A, B: Taxonomic β diversity. C, D: Functional β diversity. E, F: Phylogenetic β diversity. Solid lines show significant relationships based on Multiple Regression models on distance Matrices (shading, 95% CI). Gray bars represent 95% Bayesian credible intervals of posterior mean estimates of β diversity. See Supplementary Table S4 for related results.

functional and phylogenetic β diversity, but not taxonomic β diversity, increased significantly with differences in island isolation (F_{obs}, $P<0.01$, P_{obs}, $P<0.01$, T_{obs}, $P>0.05$; Figure 3; Supplementary Table S4). However, after correcting for imperfect detection, all β diversity measures (T_{est}, F_{est}, and P_{est}) showed significant relationships with isolation ($P<0.01$) (Figure 3; Supplementary Table S4). The extent of overestimation in both functional and phylogenetic β diversity increased significantly with differences in island area ($\Delta\beta_{\mathrm{F}}$, $P<0.05$, and $\Delta\beta_{\mathrm{P}}$, $P<0.001$), whereas overestimation in taxonomic β diversity ($\Delta\beta_{\mathrm{T}}$) was marginally significant ($P=0.053$) (Supplementary Table S5). No significant relationships ($P>0.05$) were detected between the extent of overestimation ($\Delta\beta_{\mathrm{T}}$, $\Delta\beta_{\mathrm{F}}$, and $\Delta\beta_{\mathrm{P}}$) and differences in island isolation (Supplementary Table S5).

Simulations

Simulation analyses reinforced and extended the empirical findings, demonstrating that whether β diversity (taxonomic, functional, and phylogenetic) is overestimated or underestimated under imperfect detection depends on the compositional status of undetected species between paired assemblages (i.e., shared or unique). This pattern was consistent across β diversity metrics derived from incidence-based indices (Sørensen and Jaccard indices) and abundance-based indices (Bray-Curtis index) (Figure 4; Supplementary Figures S5A, S6). When shared species were more likely to go undetected, β diversity was overestimated, indicating that assemblages appeared more dissimilar than they actually were. Conversely, when unique species were more likely to go undetected, β diversity was underestimated (Figure 4; Supplementary Figures S5A, S6).

The simulations further confirmed that imperfect detection can obscure or distort relationships between β diversity and island characteristics (Supplementary Figures S7, S8). Across all dimensions of β diversity, imperfect detection altered both the direction and strength of associations between β diversity and differences in island area and isolation. These effects persisted across all simulation scenarios, including those incorporating imperfect detection driven by species composition, traits, or phylogeny (Supplementary Figures S7, S8).

Results also indicated that, regardless of variations in the number of survey sites (seven or 36), community size (77 or 150 species), or mean and variance of detection and occupancy probabilities, taxonomic β diversity tended to be systematically overestimated (Figure 5). Increasing the number of replicated surveys per site from one to seven progressively reduced this overestimation, with estimates converging toward true values (Figure 5). Under the ideal scenario (Figure 5: Community type 1), overestimation of taxonomic β diversity declined from approximately 70% with a single survey to nearly 0% with seven replicates. Non-ideal scenarios (Figure 5: Community types 6 and 7) showed similar improvements with increased sampling effort, although the extent of bias reduction varied among scenarios.

The effectiveness of additional sampling was contingent upon other study design parameters, notably the mean and variance of detection and occupancy probabilities. In communities with low average detection probability (Figure 5: Community type 5), bias persisted (20%) even after seven replicates. In communities characterized by high variability in detection (Figure 5: Community type 4) or occupancy probabilities (Figure 5: Community type 2), bias declined more gradually, requiring 5–7 replicates to reach near-zero levels. In contrast, in communities with low average occupancy probability (Figure 5: Community type 3), even moderate sampling effort substantially reduced bias.

DISCUSSION

Incorporating imperfect detection into biodiversity estimation has become a fundamental requirement in community ecology and biogeography (Jarzyna & Jetz, 2016). Although numerous studies have addressed detectability in estimating α and γ diversity using occupancy models, there are very few studies of how imperfect detection biases β diversity estimates (Jarzyna & Jetz, 2017). Especially, few studies have explored the extent of bias in β diversity estimates along environmental

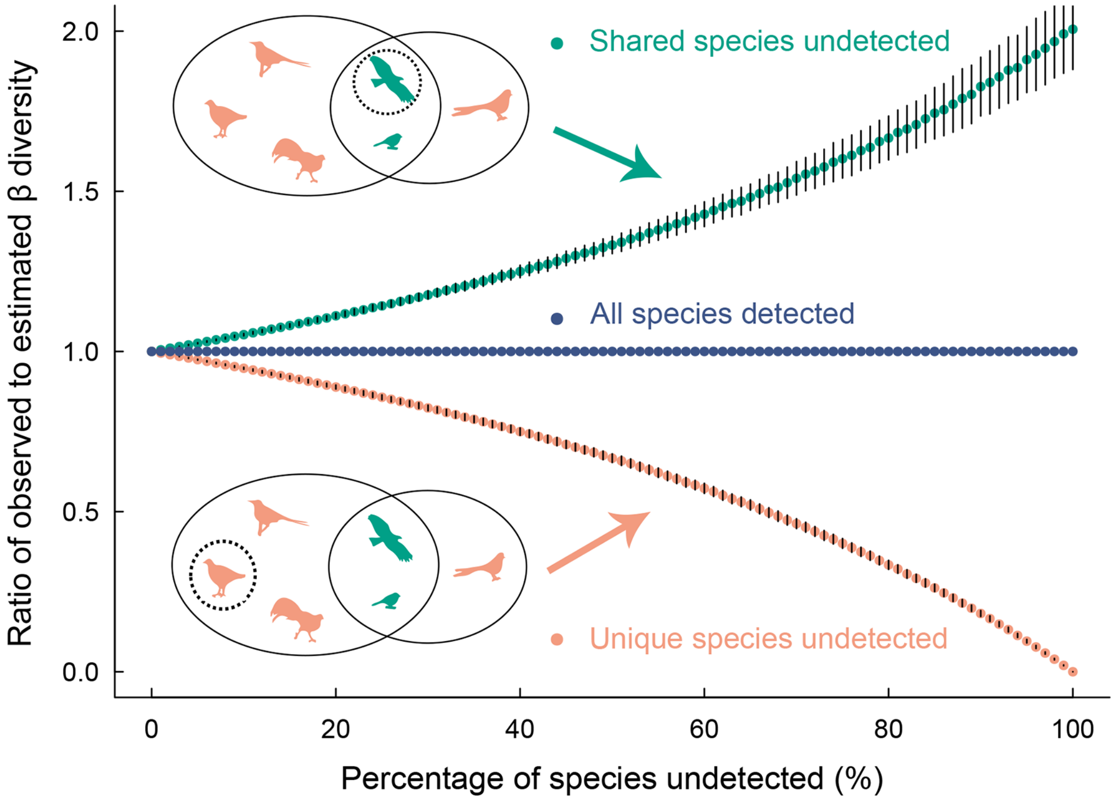

Figure 4 Simulations of taxonomic β diversity under imperfect detection by removing species based on species compositional status (i.e., shared or unique species between assemblages)

X-axis denotes percentage of species undetected, undetected from one species to all species. Y-axis denotes ratio of observed to estimated β diversity. Mean and standard deviation of β diversity were calculated from 1 000 samples across each scenario, i.e., undetected shared species (green dot), undetected unique species (orange dot), and estimated values (blue dot) of all species perfectly detected, respectively. See Supplementary Appendix S3 for further details.

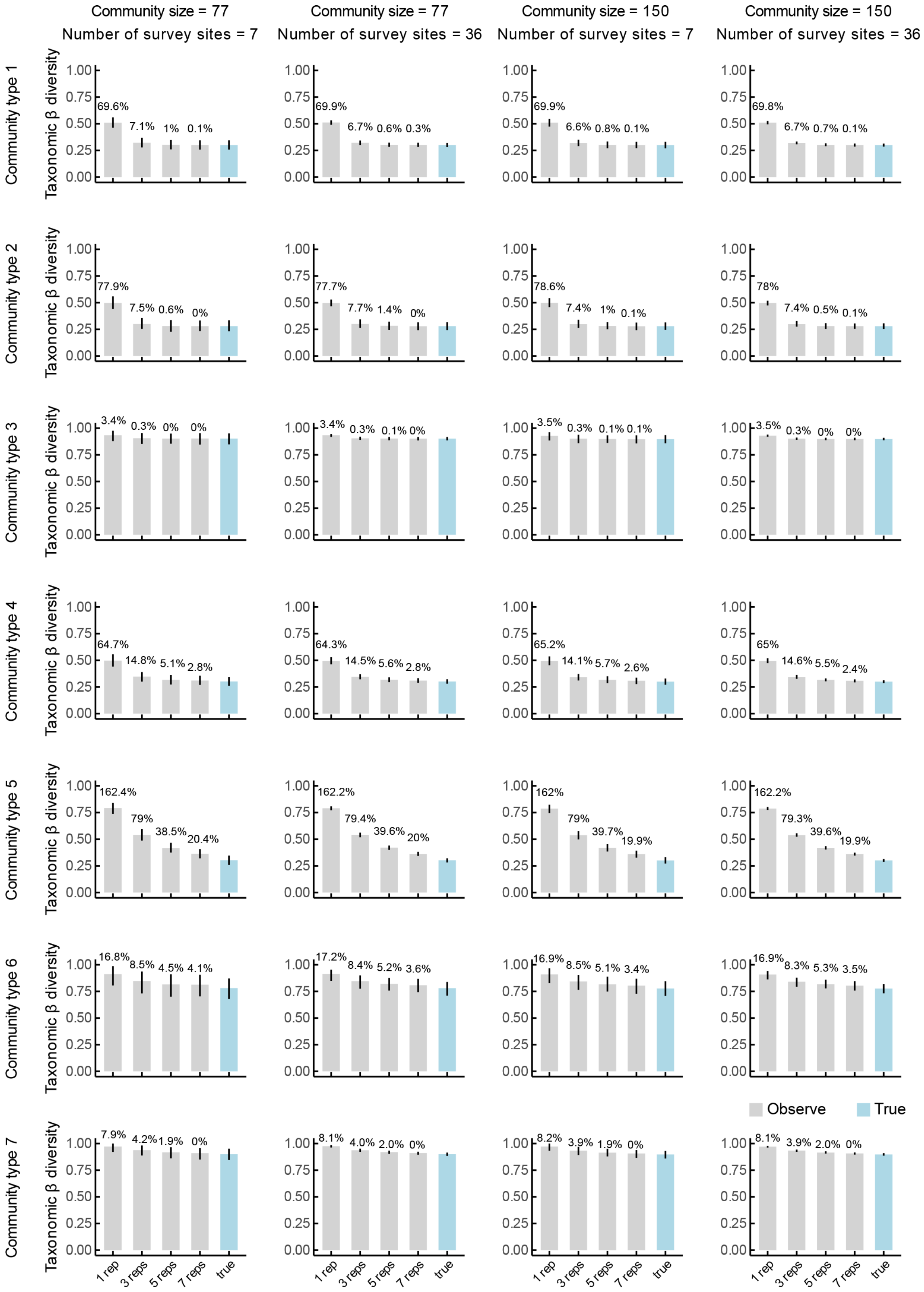

Figure 5 Simulations of taxonomic β diversity under varying study designs (i.e., number of survey sites, number of replicated surveys at each survey site) and community characteristics (e.g., community size, mean and variance of detection and occupancy probabilities), measured by the Sørensen dissimilarity index

Each column contains scenarios with varying community sizes and number of survey sites. Each row is a scenario based around communities with different means and variances of detection and occupancy probabilities. Extent of bias in taxonomic β diversity estimates was determined under all scenario combinations, varying number of survey sites, number of replicated surveys at each site, community size, and mean and variance of detection and occupancy probability (i.e., community type). In each plot, "true" taxonomic β diversity (light blue) is shown relative to "observed" taxonomic β diversity under each scenario (light gray bars). Percentages denote extent of bias of each taxonomic β diversity estimate. See Supplementary Appendix S3 for further details.

gradients or how bias differentially impacts functional or and phylogenetic estimates of β diversity.

In this study, simulations demonstrated that overlooking imperfect detection in biodiversity studies can substantially bias estimates of taxonomic, functional, and phylogenetic β diversity, with the direction of bias determined by whether undetected species are shared among or unique to assemblages. Empirical assessment of bird communities on islands in Thousand Island Lake demonstrated that shared species were more likely to go undetected, leading to overestimates of functional and phylogenetic β diversity, while taxonomic β diversity remained largely unaffected. This bias also produced erroneous inferences regarding how β diversity varied with island attributes. Results thus revealed that the effects of imperfect detection on β diversity estimates are dependent on species compositional status between assemblages (i.e., shared or unique species), and that this effect can be profound when undetected species are non-randomly distributed with respect to species-specific traits or lineages. Although empirical analysis employed a single β diversity calculation, simulation experiments confirmed that the direction and pattern of bias were consistent across multiple dissimilarity indices, including the classical Jaccard dissimilarity index and Bray-Curtis index (Supplementary Figures S5A, S6).

Analyses demonstrated that undetected shared species drove the overestimation of taxonomic, functional, and phylogenetic β diversity in bird assemblages. However, the question then arises: why are shared species more prone to non-detection than unique ones? In the empirical dataset, detectability among shared species showed significant negative correlations with body mass and body length (Supplementary Figure S4A, B). Large-bodied birds such as *Falco tinnunculus* and *Eudynamys scolopaceus* were more frequently overlooked than smaller species such as *Zosterops japonicus* and *Pomatorhinus ruficollis*. Although larger species possess higher dispersal ability, allowing them to occupy multiple islands, their preference for dense vegetation or canopy cover, combined with infrequent vocalization, reduces detectability. Consequently, these species are both more likely to be shared across islands and more likely to remain undetected during surveys.

While empirical evidence demonstrated that shared species were more likely to go undetected, leading to overestimations of taxonomic, functional, and phylogenetic β diversity, the extent of bias varied among diversity dimensions. Imperfect detection of shared species led to a significant overestimation of functional and phylogenetic β diversity but not taxonomic β diversity (Figure 2; Supplementary Table S2). Among the 630 island pairs examined, only 55.4% exhibited overestimated taxonomic β diversity, compared with more than 90.0% showing overestimation in functional and phylogenetic β dimensions (Supplementary Table S6). The strong congruence between functional and phylogenetic bias under imperfect detection was largely attributed to evolutionary conservatism of ecological traits, resulting in a similar pattern between functional and phylogenetic β diversity (Swenson, 2011, 2014). However, the weaker correspondence between taxonomic β diversity and the other two dimensions likely arises from differences in how species are distributed across taxonomic, functional, and phylogenetic spaces (Swenson, 2014), consistent with our prediction that bias in β diversity estimates may be affected systematically by species traits and evolutionary histories.

Imperfect detection not only distorted β diversity estimates but also obscured the underlying ecological relationships linking β diversity to key fragmentation gradients in the island system. Using uncorrected data, both phylogenetic (Figure 3E; Supplementary Table S4) and functional (Figure 3C; Supplementary Table S4) β diversity showed positive associations with differences in island area; however, these associations weakened or even reversed once detection bias was corrected. Larger islands typically support higher species turnover due to enhanced richness and habitat heterogeneity (James et al., 2012), yet such ecological signals can be obscured by reduced detectability within structurally complex habitats. Notably, although taxonomic β diversity estimates were not strongly biased (Figure 2A; Supplementary Table S2), correcting for imperfect detection revealed a significant relationship with island isolation that was obscured in the observed data (Figure 3B; Supplementary Table S4)—highlighting that environmental drivers of β diversity can be substantially masked when detection errors are ignored, even if diversity metrics themselves appear stable. Consistent with earlier research in the same lake system (Si et al., 2016), the corrected analysis revealed that the influence of island isolation on β diversity only emerged after accounting for imperfect detection (Figure 3B, D, F; Supplementary Table S4), reflecting how dispersal limitation intensifies compositional turnover (Liang et al., 2024). These results emphasize that apparent stability in observed diversity patterns may be misleading and that true biodiversity–environment relationships become evident only after accounting for imperfect detection. While the empirical analysis primarily addressed the impact of undetected species, the simulation results provided broader insights into how imperfect detection can bias biodiversity-environment relationships (Supplementary Figures S7, S8).

The extent (or magnitude) of bias in β diversity estimation varied systematically with island attributes. After accounting for imperfect detection, the extent of overestimation in taxonomic, functional, and phylogenetic β diversity increased significantly with differences in island area (Supplementary Table S5). This trend likely reflects the greater environmental heterogeneity and species richness of large islands, which accommodate more species that are shared with other islands (James et al., 2012). However, detectability conditions are often more complex on large islands due to the diversity of microhabitats, such as dense understory or multilayered canopies, that hinder visual and acoustic detection. Thus, when comparing islands that differ markedly in area, imperfect detection amplifies perceived dissimilarity and inflates β diversity estimates.

Collectively, these findings underscore the importance of accounting for imperfect detection to uncover how different dimensions of biodiversity—taxonomic, functional, and phylogenetic—respond to environmental gradients. Taxonomic β diversity appeared comparatively robust to imperfect detection, whereas functional and phylogenetic β diversity were more susceptible to biases arising from the non-detection of species with unique traits or deep evolutionary histories. This pattern suggests that niche-based processes such as environmental filtering exert a stronger influence on functional and phylogenetic turnover. Undetected species that occupy unique ecological or evolutionary positions may thus distort assessments of community structure (Si et al., 2018).

Moreover, the altered relationships between β diversity and island attributes highlight that uncorrected detection errors can obscure or misrepresent interpretations of community dynamics.

The simulation analyses not only corroborated the empirical findings but also revealed broader mechanisms by which detection biases alter estimates of β diversity, providing practical recommendations for optimizing field survey design. Increasing the number of replicated surveys within a primary sampling period markedly mitigated bias, with overestimation gradually decreasing as replication increased. This trend was consistent across both ideal and non-ideal communities (Figure 5). When replication was sufficiently high, β diversity estimates approached unbiased values even without explicit model-based correction (Figure 5). Nevertheless, logistical and financial constraints often limit extensive repetition in field surveys, and the optimal replication effort varies according to community characteristics (Figure 5).

Although occupancy models were applied in this analysis, both non-parametric (Chao et al., 2023) and parametric frameworks have the capacity to correct β diversity estimates under conditions of imperfect detection. Non-parametric estimators can infer the total number of undetected species (Chao et al., 2006; Zou & Axmacher, 2021) but do not identify which species are missing. This limitation is critical for functional and phylogenetic diversity, which convey ecologically and evolutionarily informative dimensions beyond species counts (Cadotte et al., 2011) and therefore rely on explicit knowledge of species identities that define ecological roles and lineage structure. Occupancy models provide a distinct advantage in this regard, enabling identification of specific undetected species and facilitating not only more accurate β diversity estimation but also deeper insight into how non-detection of particular taxa may bias diversity patterns.

Although the simulation framework explored a range of β diversity metrics, including those incorporating abundance, the empirical analyses were necessarily restricted to incidence data and the selected indices. While abundance data can yield more detailed ecological insights than occupancy data, the latter remain far more accessible and practical to obtain across taxa and regions (Dorazio et al., 2011; Mackenzie et al., 2002). Nevertheless, given that abundance itself can bias detection probability (Royle & Nichols, 2003), future research should assess how variation in abundance impacts β diversity estimation. Further investigation is also needed to explore the sensitivity of β diversity metrics to imperfect detection in the context of different β diversity metrics, including dissimilarity and multiplicative indices (Barwell et al., 2015; Ke et al., 2023).

In conclusion, imperfect detection was shown to bias all dimensions of avian β diversity through the non-random distribution of undetected species across assemblages. Analyses revealed that species-specific detection bias, correlated with traits such as body size, inflated β diversity estimates derived from raw data, particularly for functional and phylogenetic metrics that depend on species identity. Although not all empirical studies will necessarily suffer severe bias, the potential for imperfect detection to distort β-diversity patterns warrants explicit consideration, especially for taxa such as birds that frequently evade observation. Replicated surveys within each site remain the most reliable means of minimizing such bias—both by reducing bias in accumulated data and by facilitating detection-correction methods—although the optimal number of replicated surveys depends on the distribution of occupancy and detection probabilities in a given community.

DATA AVAILABILITY

The data that support the findings of this study are openly available in Figshare at https://figshare.com/s/8e557bcd730119789130.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

X.S. conceived the study idea; X.S. and P.D. designed the study; X.S., D.Z., Y.Z., and P.D. collected field data; D.Z., Y.Z., M.W.T., M.W.C., P.D., and X.S. commented on the manuscript. Y.W. analyzed the data and led the writing. All authors read and approved the final version of the manuscript.

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