

TECHNICAL ADVANCE

If You're Rare, Should I Care? How Imperfect Detection Changes Relationships Between Biodiversity and Global Change Drivers

Ana Miller-ter Kuile^{1,2}  | An Bui³  | Austen Apigo⁴  | Shelby Lamm¹  | Megan Swan⁵  | Jamie S. Sanderlin²  | Kiona Ogle¹ 

¹Northern Arizona University, School of Informatics, Computing and Cyber Systems, Flagstaff, Arizona, USA | ²USDA Forest Service Rocky Mountain Research Station, Flagstaff, Arizona, USA | ³University of California, Santa Barbara, Department of Ecology, Evolution, and Marine Biology, Santa Barbara, California, USA | ⁴University of California, Irvine, Department of Ecology and Evolutionary Biology, Irvine, California, USA | ⁵National Park Service Southern Colorado Plateau Inventory and Monitoring Network, Flagstaff, Arizona, USA

Correspondence: Ana Miller-ter Kuile (ana.miller-ter-kuile@nau.edu)

Received: 9 April 2025 | **Revised:** 26 June 2025 | **Accepted:** 9 July 2025

Funding: This work was supported by Rocky Mountain Research Station, Challenge Cost Share 21-CS-11221635-194.

Keywords: bray–Curtis dissimilarity | functional richness | grasshoppers | multi-species abundance model | multi-species occupancy model | passerine birds | stability | understory plants

ABSTRACT

Across ecosystems and biomes, most species in biological communities are rare. Many studies discount rare species when examining biodiversity patterns, assuming that common species are most influential for ecosystem functioning. There is growing evidence, however, that rare species contribute unique functions in many ecosystems; thus, discounting them produces misleading conclusions about how biodiversity is changing in the face of natural and anthropogenic forces. Rare species are more likely to be missed by multi-species sampling designs and are thus particularly vulnerable to detection error. Best practice in biodiversity assessments should include rare species and account for error in the detection process. We outline a general approach that accounts for detection error in sampling designs using multi-species occupancy and abundance models (MSOM/MSAM). We then show how uncertainty in detection can be propagated from MSOM/MSAM results to derive more accurate estimates of alpha and beta diversity metrics. Finally, we show how uncertainty in these diversity metrics can be accounted for in follow-up regression models to evaluate relationships between biodiversity and global change covariates. Using three case studies across diverse taxa (birds, insects, and plants), we demonstrate how accounting for the detection process alters the relationships between biodiversity and global change drivers in ways that are important for understanding and predicting ongoing change in these communities. Our generalizable analysis approach can aid in accounting for rare species in studies of global biodiversity.

1 | Introduction

Most species in natural ecosystems are rare (Rabinowitz 1981; Figure 1). Historically, rare species have often been excluded from analyses of biodiversity under the assumption that more abundant or common species contribute most to ecosystem functioning (Poos and Jackson 2012; Sasaki and Lauenroth 2011). But, there is

growing evidence that rare species are important for understanding relationships between biodiversity and ecosystem functioning and services (Dee et al. 2019; Mouillot et al. 2013). For example, rare species disproportionately influence functional diversity (Jain et al. 2014; Leitão et al. 2016; Roth et al. 2018) since these species often have unique trait combinations (e.g., large-bodied long-distance seed dispersing birds in Australia; Leitão et al. 2016).

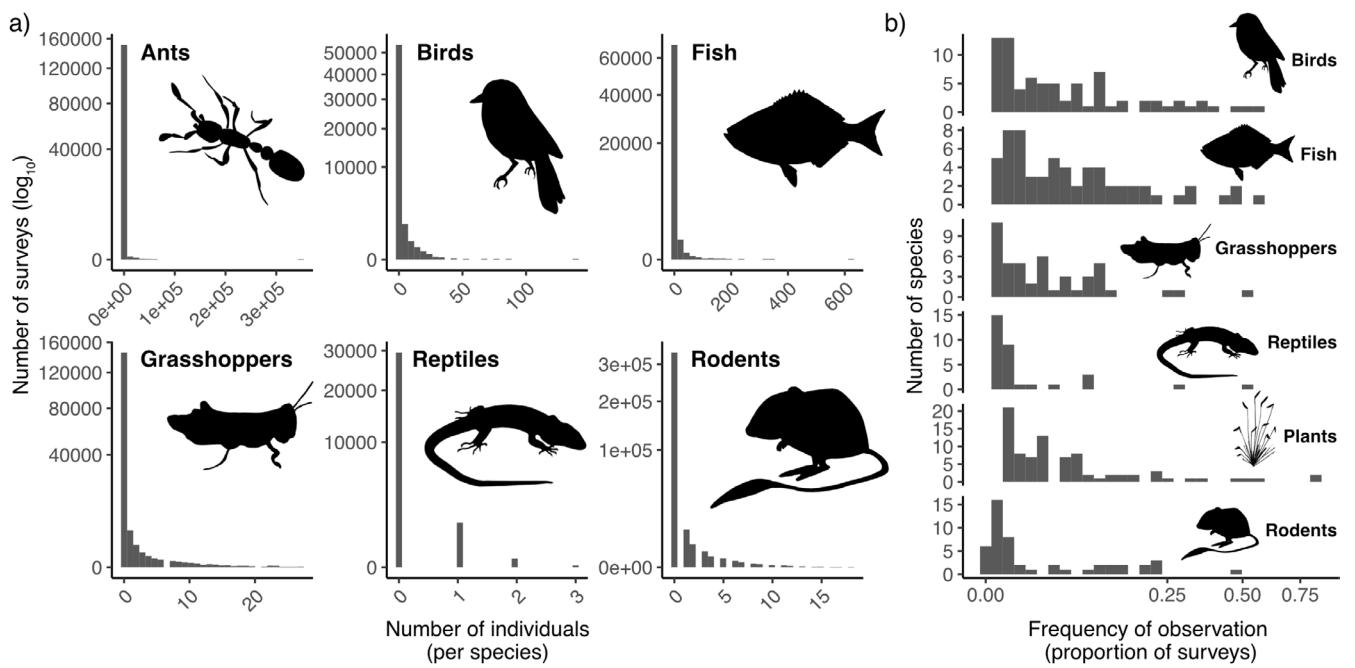


FIGURE 1 | Two dimensions of rarity that highlight that rarity is the norm in ecosystems across the globe. Here, we show that most species are (a) rare in abundance across sampling surveys and (b) detected in relatively few sampling sessions. We demonstrate this general pattern for a diversity of taxa across systems, including terrestrial and marine animals and plants. (Data from: Bateman and Childers 2024; Boyle 2023; Gibb et al. 2017; Lightfoot 2021; Morgan Ernest et al. 2022; Reed and Miller 2022; Swan and Plough 2023).

Thus, including rare species in biodiversity assessments may fundamentally change our understanding of how ongoing global change will shape ecosystems (Jaureguiberry et al. 2022).

Incorporating rare species into biodiversity metrics may alter predictions about many facets of biodiversity since rare species may have unique responses to environmental perturbations (Säterberg et al. 2019). However, many multi-species observational datasets, even those with long temporal or broad spatial coverage, do not incorporate survey designs to capture rare or patchy species distributions (Devarajan et al. 2020; Jeliazkov et al. 2022; Sanderlin et al. 2014; Zipkin et al. 2010). As a result, many multi-species sampling methods are likely to systematically miss rare species. A challenge to incorporating rare species is the possibility of “false negatives”: species or individuals are present but considered absent because they are not detected during a survey (Zipkin et al. 2010). Thus, when we examine biodiversity patterns to identify environmental factors influencing biodiversity, our analyses may be biased by weaknesses of the sampling design, making it challenging to discover real biological patterns. Not considering rare species in biodiversity-global change assessments may alter our predictions of the direction, magnitude, and timescales of influence of global change drivers.

Biodiversity assessments could benefit from accounting for imperfect detection of species, especially those that are rare. We outline a general approach that leverages established modeling methods that account for imperfect detection (Bayesian multi-species occupancy and abundance models; Dorazio et al. 2006; Iknayan et al. 2014) to generate unmeasured (“latent” or “true”) abundance and occupancy estimates from observed data with detection error. We then show how these “true” estimates can subsequently be used to generate biodiversity metrics (both alpha and

beta diversity), thus propagating uncertainties associated with the detection error process to accurately describe diversity patterns. Diversity estimates (mean and variance) can be subsequently analyzed via regression models that explicitly incorporate variance as a measure of uncertainty to evaluate how potentially important covariates impact community diversity. Regression modeling can also incorporate the lagged effects of environmental drivers using a stochastic antecedent modeling framework (Ogle et al. 2015; Figure 2). Using this multi-step process, we demonstrate how accounting for imperfect detection of all species (especially rare species) alters estimates of global change driver effects—direction, magnitude, and timescales of influence—using three examples of long-term community datasets representing a variety of taxa (plants, invertebrates, and vertebrates).

2 | Materials & Methods

2.1 | Overview of Modeling Process

Our modeling framework examines relationships between environmental covariates and biodiversity following a two-part process (Figure 2). First, we modeled latent (“true”) abundance or occupancy for all species in a community using either a multi-species abundance (“MSAM”) or occupancy (“MSOM”) model (Dorazio et al. 2006; Iknayan et al. 2014). We extended the MSAM and MSOM approach by simultaneously computing derived values for indices of biodiversity (including alpha and beta diversity aspects of both taxonomic and functional diversity). Then, we used the posterior mean and standard deviation estimates of the biodiversity indices in a subsequent beta-regression model (da Silva et al. 2018) to examine the concurrent and lagged effects of environmental

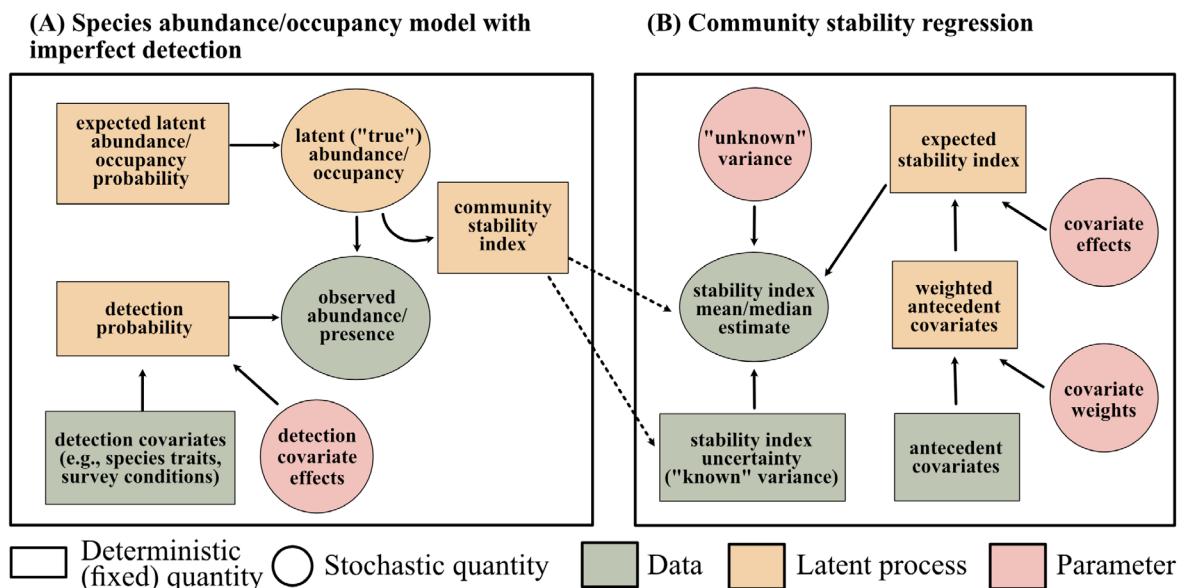


FIGURE 2 | A simplified graphical model illustrating data, latent processes, and parameters associated with the (A) multi-species abundance (or occupancy) model (MSAM or MSOM) that accounts for imperfect detection associated with the observed data (e.g., observed abundance, species counts, or presence/absence), which produces posterior estimates of community change and associated estimates of uncertainty, which are in turn treated as data in the (B) beta-regression model that evaluates the effects of environmental drivers and their timescales of influence on biodiversity. Models in (A) and (B) account for hierarchical or nested sampling schemes by incorporating random effects for time (e.g., year effects) and location (e.g., transect, plot, and/or site effects). Covariates used in (A) include variables that potentially affect the probability of detection (e.g., environmental conditions or species-trait affecting detection ability), and covariates used in (B) represent time-varying biotic or abiotic drivers that likely affect diversity, and for which antecedent terms are computed as weighted averages of concurrent and past observed covariate data. A more detailed version of this figure can be found in Figure S5.

variables on biodiversity (Ogle et al. 2015). Below, we provide more details on each modeling step and the datasets we used to illustrate its utility. Further details can be found in the Supporting Information and in our online tutorial (https://anbui.github.io/community_detection_tutorial/).

2.2 | Accounting for Detection Error

Accounting for detection error in observational datasets of species occurrence or abundance is not a new concept (e.g., Dorazio et al. 2006; Kéry and Schmidt 2008; MacKenzie et al. 2002; Royle et al. 2005). Across fields, researchers have acknowledged that it can be difficult to detect all components (e.g., species) in ecosystems and have proposed a suite of approaches for dealing with this problem. For multi-species datasets, it is common to use multi-species occupancy and abundance models (MSOM/MSAM) that “correct” observed data to estimate latent (i.e., variables that are either not observed or partially observed) “true” values of occurrence (occupancy) or abundance. These models typically include two parts: (1) an observational process model that accounts for uncertainty in the observed data using covariates that could alter detection probabilities, and (2) a biological process model that is informed by the detection error process in (1), producing latent (unmeasured) “true” occupancy or abundance estimates that can, in turn, be modeled as a function of environmental and biological covariates (Figure 2). These models allow rarer species in a community to “borrow strength” from more common species by allowing species-level parameters to be modeled hierarchically around community- or group-level

parameters (Iknayan et al. 2014; Ogle et al. 2013). These models account for “false negatives” and generally shift latent species abundance and frequency distributions to higher values relative to observed values (Figure 3). Further, while we focus on rare species in this study, these methods also better quantify occupancy and abundance of species that may not be rare but are hard to detect due to cryptic behavior or markings (Garrard et al. 2013). The MSOM/MSAM approach has been applied often in studies of vertebrate communities (Kellner and Swihart 2014) but is not common practice in community ecology, especially for invertebrates and plants; but see (Chen et al. 2013; Lamouille-Hébert et al. 2025). Moreover, there is an opportunity to use the species-level latent abundance or occupancy estimates to produce realistic estimates of biodiversity that account for detection errors at the species level, but aside from a few studies focusing on species richness (Dorazio et al. 2006; Tingley et al. 2020), this approach has generally not been applied to other diversity metrics; but see (Broms et al. 2015; Cannon et al. 2019; Si et al. 2018 e.g., for both taxonomic and functional alpha diversity metrics other than species richness). The structure of these models is explained thoroughly in original literature (e.g., Dorazio et al. 2006; MacKenzie et al. 2002; Royle et al. 2005) and our application of them can be found in the (Supporting Information).

2.3 | Generating Values of Alpha and Beta Diversity

Once detection errors have been accounted for via a MSOM or MSAM, the latent (“true”) occupancy and abundance of

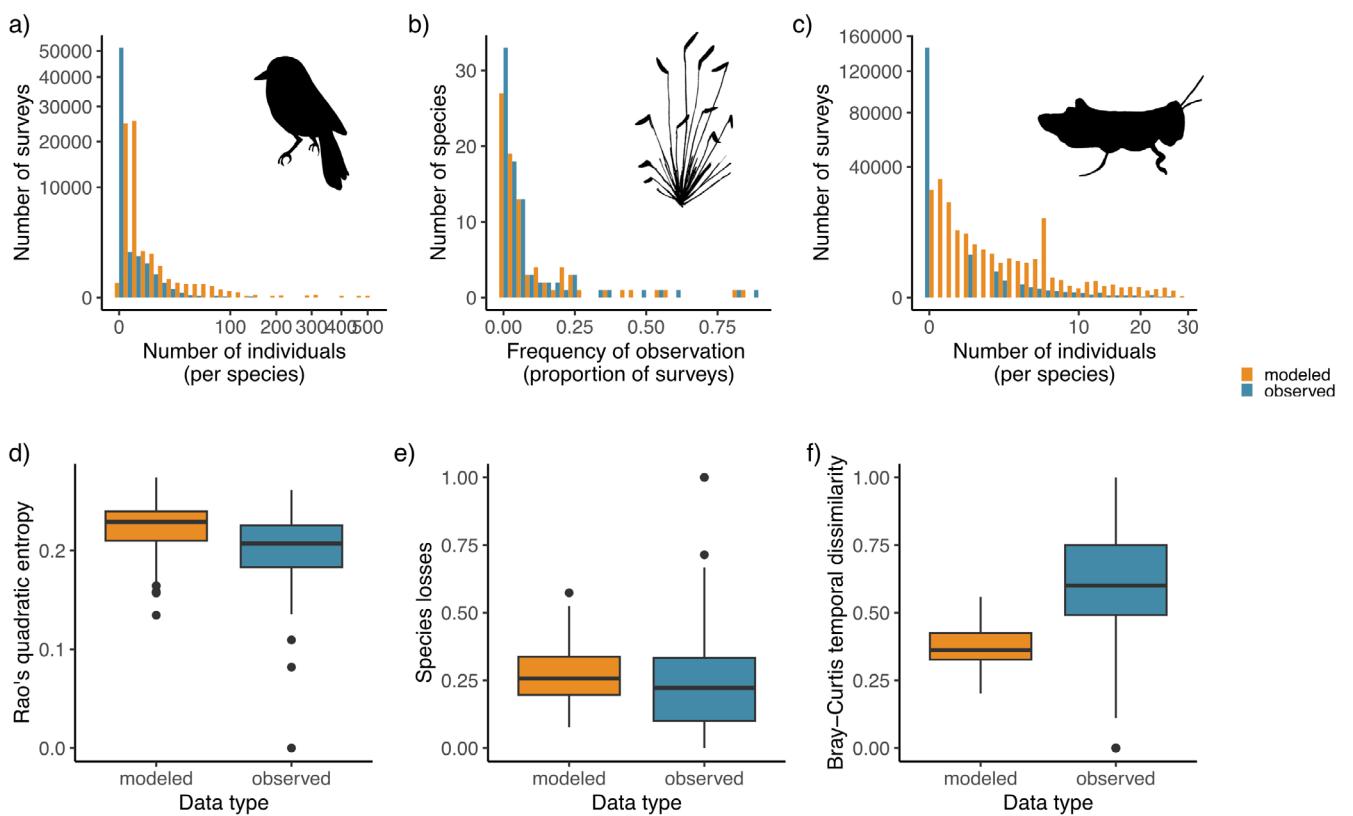


FIGURE 3 | Distributions of abundances and occurrence when ignoring (blue) or accounting for (yellow) detection error for three example datasets: (a) birds at the Konza Prairie Long-term Ecological Research Site, Kansas, USA (Boyle 2023), (b) plants at Petrified Forest National Park, Arizona, USA (Swan and Plough 2023), and (c) grasshoppers at the Sevilleta Long-term Ecological Research Site, New Mexico, USA (Lightfoot 2021). Results show how accounting for imperfect detection alters estimates of a variety of biodiversity metrics based on abundance for (d) birds (Rao's quadratic entropy), occurrence for (e) plants (species turnover) and abundance for (f) grasshoppers (Bray–Curtis dissimilarity). In all three, accounting for imperfect detection shifts species abundance and occurrence distributions to the right (a–c) compared to the observed data that ignores detection errors. Accounting for rare species leads to (d) increases in bird functional diversity, (e) increases in the number of plant species lost over time, and (f) decreases abundance-based dissimilarity for grasshoppers.

each species in a community can be used to generate a variety of biodiversity metrics common in community ecology, including measures of alpha and beta diversity based both on occurrence and abundance values (e.g., taxonomic and functional diversity metrics such as Bray–Curtis and Jaccard dissimilarity and Rao's quadratic entropy; (Baselga 2013; Botta-Dukát 2005; Cannon et al. 2019; Hallett et al. 2016; Morris et al. 2014; Oksanen et al. 2020); Figure 3). Further, occupancy probabilities can also be used as a proxy for relative abundances (e.g., Broms et al. 2015). The Bayesian statistical framework in which these models are commonly implemented draws from the posterior to generate a set of independent samples for all stochastic quantities of interest, including the latent abundance or occupancy values (or probabilities). Via analysis of the posterior distributions, resulting biodiversity metrics can be described in terms of both their central tendency (mean or median) and their variance or uncertainty (e.g., standard deviation, Bayesian credible intervals; Ellison 2004). Greater detail on biodiversity metrics can be found in the original literature describing them (e.g., Baselga 2013; Botta-Dukát 2005; Cannon et al. 2019; Hallett et al. 2016; Morris et al. 2014; Oksanen et al. 2020) and can be found in the (Supporting Information).

2.4 | Evaluating Drivers of Biodiversity Patterns

Many diversity indices (including alpha and beta diversity) are defined on the [0,1] interval (Oksanen et al. 2020). Thus, we describe a general Bayesian model framework that uses a beta distribution to model the stochastic diversity indices (Ferrari and Cribari-Neto 2004; Irvine et al. 2016). Importantly, the uncertainty in estimates of biodiversity generated from multi-species models is propagated to these downstream analyses. Further, because biodiversity responses to environmental drivers stem from complex population and community processes related to resource availability, competition, species-specific life history, and food web dynamics, among others, it is likely that biodiversity could have a lagged response to potential drivers (Essl et al. 2015a, 2015b; Figueiredo et al. 2019; Thompson and Ollason 2001). We can explicitly test for these lagged responses by combining the beta data model with a stochastic antecedent model (SAM) that provides estimates of covariate effects, where the covariates are, in turn, modeled as a weighted average of concurrent and past values. Each lag period gets an estimated importance weight describing its relative influence on the biodiversity response (Ogle et al. 2015). These lagged responses can be set at a variety of timescales (e.g., days, weeks,

seasons, years) depending on the biology of the organisms in a community.

In the beta-regression model, we treated the posterior mean biodiversity metric for a site and year as the response variable and accounted for uncertainty in these values via the posterior standard deviation by partitioning variance in the model into “known” variance (the posterior standard deviation) and additional unknown variance that describes additional variability in the biodiversity indices that is not explained by the environmental covariates. We modeled the mean or expected diversity index using the beta regression with an intercept and coefficients for the effects of each antecedent covariate in the SAM model. Each time-varying antecedent covariate represents a weighted average of the current value (at the time concurrent with y) and past values preceding time y . The importance of each time lag to the overall covariate effect is defined by an importance weight. We assigned the vector of importance weights for a given covariate a relatively non-informative Dirichlet prior so that these weights sum to 1 across all lags. Thus, when a covariate effect is significant, the weights for each time lag for that covariate lend insight into the timescale(s) over which that covariate influences biodiversity. This approach builds on existing approaches (Ferrari and Cribari-Neto 2004; Irvine et al. 2016; Ogle et al. 2015) but is novel in incorporating the additional “known” uncertainty from the MSOM/MSAM models and can be found in the (Supporting Information).

2.5 | Applying the Combined Modeling Framework

To evaluate the importance of detection error, we derived values of biodiversity for three examples in two ways: (1) using observational data ignoring detection error and (2) using the above modeling framework. These examples examined how accounting for imperfect detection alters predictions of the direction, magnitude, and temporal scale of effects of environmental covariates on multiple biodiversity metrics across a diverse range of environments and biological communities. Any differences stemmed largely from the inclusion of rare species. Our aim was not to provide comprehensive ecological analyses of these communities, but rather, to illustrate the utility of the combined modeling approach.

We chose gold-standard, long-term ecological survey and monitoring data that met the assumptions for multi-species models (e.g., multiple surveys within “closed” timeframes) and that had sufficient temporal coverage (15–20+ years) to examine the influence of long-term variability in climate drivers. For all three examples, we chose alpha and beta diversity metrics that are common in the field (e.g., used widely in the R package *vegan*; Oksanen et al. 2020), and/or that highlight the general utility across dataset types (presence vs. abundance) and taxonomic and functional facets of biodiversity. These represent a subset of the full potential of biodiversity metrics and are meant to highlight the consistent importance of imperfect detection across systems and metrics. Choice of metrics will depend on the goals of specific studies and often a combination of metrics will paint a more complete picture of biodiversity and change (Carroll et al. 2025; Morris et al. 2014). Further, all datasets represented surveys that captured >95% of the total species pool

likely present in each meta-community, based on rarefaction (Figure S1), thus allowing us to calculate diversity metrics based on a known species pool (Tingley et al. 2020). The Supporting Information provides details on the data processing for all three examples and results for several additional diversity metrics (Figures S2–S4). Code and data can be found online (Miller-ter Kuile et al. 2025).

2.6 | Case Studies

2.6.1 | Functional Richness of Bird Communities at the Konza Prairie Long-Term Ecological Research (LTER) Site, Kansas, USA

Functional diversity metrics describe communities in terms of how the organisms in that community contribute to ecosystem functions such as nutrient cycling and storage (Mammola et al. 2021). Studies have shown that rare species are important for these metrics (Leitão et al. 2016; Mouillot et al. 2013), since rare species can often represent unique trait combinations (i.e., larger animals are rarer and disperse larger seeds; Donoso et al. 2020).

In this example, we examined Rao's quadratic entropy, an abundance-based metric of functional richness of grassland passerine bird communities at Konza Prairie LTER, Kansas, USA (Boyle 2023; Bruckerhoff et al. 2020; Nippert 2023; Tobias et al. 2022). This community comprised 78 distinct species and we compiled traits using a set of traits from the AVONET trait database (Cannon et al. 2019; Tobias et al. 2022). In the beta-regression, we considered the covariates of temperature and cumulative precipitation, using daily weather station data collected at the KNZ LTER headquarters (Bruckerhoff et al. 2020; Nippert 2023). We compiled these data at a seasonal scale (“cold, dry”: October–March and “warm, wet”: April–September). We considered the effect of the concurrent season (always the “cold, dry”) and the preceding five seasons.

2.6.2 | Occurrence-Based Dynamics of Plant Communities in Petrified Forest National Park, Arizona, USA

Community dynamics can alter ecological stability (e.g., how ecosystems support ecosystem functions) through time (Loreau and de Mazancourt 2013). One way of quantifying community dynamics is through changes in species occurrence over time (“turnover” or “nestedness”; Baselga 2013), which can be partitioned into local extinction and colonization (Hallett et al. 2016). Rare species are more likely to go locally extinct due to small population sizes and relative isolation from other conspecific patches (e.g., Matthies et al. 2004); therefore, improved estimation of their presence helps to better represent local extinction events.

In this example, we examined temporal patterns of species losses based on occurrence data for understory plants in Petrified Forest National Park, Arizona, USA. These data come from the National Park Service's Inventory and Monitoring program (Swan and Plouffe 2023). This community consists of 84 species of grasses,

forbs, shrubs, and cacti. We focused on evaluating changes in community composition through time from 1 year to the next sampling year. Data were not collected on an annual basis, so we considered the change over the reported sampling period, from y to $y + \Delta y$, where Δy was > 1 year. In the beta-regression, we considered the effects of precipitation and vapor pressure deficit (VPD), both of which are expected to be important in this semiarid system (Cowles et al. 2016). We compiled monthly climate data from PRISM (PRISM Climate Group 2014) for each survey plot and divided these data seasonally per year, with a focus on winter (November–February), spring (March–April), early summer (May–June), and monsoon (July–September). We considered the concurrent season as well as the previous seven seasons (2 years).

2.6.3 | Abundance-Based Dynamics of Grasshopper Communities at the Sevilleta LTER, New Mexico, USA

Another way temporal community dynamics are examined is through abundance-based beta diversity metrics (e.g., Bray–Curtis dissimilarity between time points at a site, Oksanen et al. 2020). While many abundance-based metrics are shaped mostly by common species (Brasil et al. 2020), better accounting for all species is likely to alter these estimates. There are many abundance-based metrics of beta diversity, and some even better weight rare species (e.g., Chao et al. 2005); however, we have chosen to use Bray–Curtis because it is a familiar and widely used metric often assumed to be insensitive to the inclusion of rare species (Anderson et al. 2011).

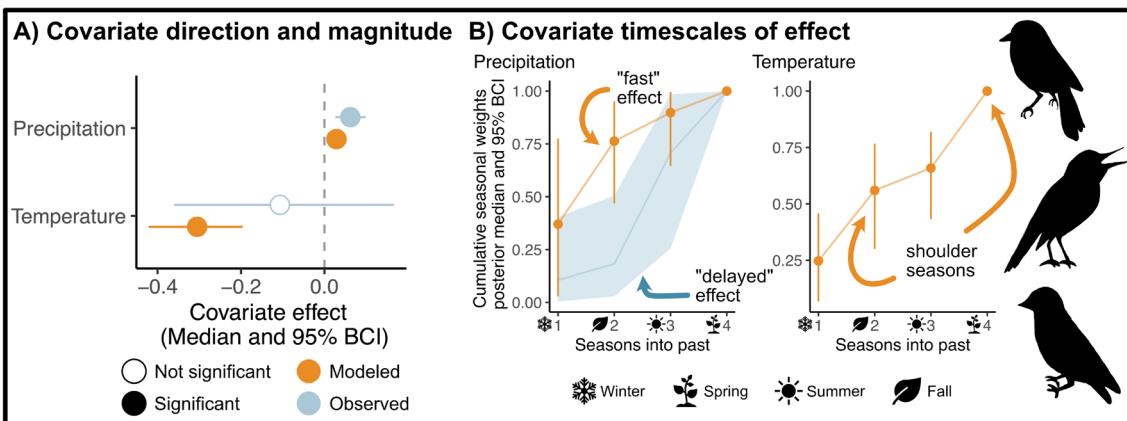
In this example, we examined temporal variability in beta diversity of grasshopper communities at Sevilleta LTER from 1992 to 2019 (Baur et al. 2022; Lightfoot 2021; Moore and Hall 2023). This community is composed of 46 species of grasshoppers. We focused on evaluating changes in community composition through time from 1 year to the next (i.e., from year y to $y + 1$). In the beta-regression, we considered the variables of mean monthly temperature, total monthly precipitation, and mean live plant biomass (Jonas et al. 2015). Climate data were collected at a weather station near both sites at an hourly timescale (Moore and Hall 2023). We summarized climate data at a seasonal timescale (temperature: “warm” [April–October] and “cool” [November–January]; precipitation: “wet” [July–October] and “dry” [November–June]). We considered the effect of the concurrent season temperature and precipitation as well as the previous five seasons. We averaged seasonal (spring and fall) plant biomass data for each year for the understory plants collected at each site (Baur et al. 2022). We considered the biomass effects of the concurrent season as well as the previous 10 seasons (five and a half years).

3 | Results & Discussion

3.1 | Functional Richness of Bird Communities at the Konza Prairie Long-Term Ecological Research Site, Kansas, USA

For bird communities in Konza Prairie LTER, Kansas, USA, functional alpha diversity measured via Rao's quadratic

Covariate direction, magnitude, and timescales for bird functional diversity



Summary and ecological implications

Ignoring detection error:

Delayed, positive precipitation effect (spring and summer)

Accounting for detection error:

Fast, positive precipitation (winter and fall) and **negative shoulder season temperature effects** (fall and spring)

Potential ecological drivers:

Abundance or diversity of food before spring breeding

Potential ecological drivers:

Early emergence of diverse food resources, changes in phenology (bird and resource), competition

FIGURE 4 | Illustration of how accounting for imperfect detection alters estimates of covariate effects and their timescales of influence on bird functional diversity measured as Rao's quadratic entropy. Data are from species abundance surveys of passerine bird species from the Konza Prairie Long-term Ecological Research (LTER) site in Kansas, USA (Boyle 2023; Nippert 2023).

entropy increased slightly when accounting for detection error (Figure 3). Rather than there being a delayed positive effect of precipitation on Rao's quadratic entropy, accounting for imperfect detection of species demonstrates that, in fact, the precipitation effect acted more quickly (Figure 4B). Further, temperature had a much stronger effect on functional diversity of grassland birds (Figure 4A) and was most important in the shoulder seasons (spring and fall; Figure 4B). Accounting for detection error shifted the ecological interpretation of patterns in this system from being a smaller set of simpler potential mechanisms, such as precipitation leading to increases in abundance or diversity of spring resources that trigger increased nest success or earlier migration (Marra et al. 2005; McKinnon et al. 2012) to a complex potential suite of mechanisms. These mechanisms could include early emergence of diverse or abundant food resources triggered by precipitation prior to the nesting season, changes or mismatches in the phenology of birds and resources (e.g., migration and emergence/germination) in warmer springs or falls, or increased competition among birds when warm spring or fall conditions lead to more limited food options (Illán et al. 2014; Kokko 1999; Studds and Marra 2011).

3.2 | Occurrence-Based Dynamics of Plant Communities in Petrified Forest National Park, Arizona, USA

For plant communities in Petrified Forest National Park, Arizona, USA, accounting for imperfect detection increased estimates of

species losses (Figure 3), likely because rare species were better accounted for in the community. When we do not account for imperfect detection, indices of moisture status—precipitation and vapor pressure deficit (VPD)—did not impact species losses in this water-limited ecosystem (Figure 5A). Conversely, when accounting for imperfect detection, both VPD and precipitation had positive effects on species loss. Both drivers had seasonal signals on species loss, with summer VPD, summer precipitation, and winter precipitation having the greatest effects (Figure 5B). High precipitation in the summer and winter can shape competitive dynamics; highly abundant annual plants may take advantage of improved access to moisture, potentially outcompeting rarer species (Kadmon 1995). The temporal signals for both VPD and precipitation extended through two summers, suggesting that dynamics of reproduction, growth, competition, and thermal or drought stress can have relatively long "memories", even in communities with shorter-lived plants (Fernández-Pascual et al. 2019; Walter et al. 2011).

3.3 | Abundance-Based Dynamics of Grasshopper Communities at the Sevilleta LTER, New Mexico, USA

For grasshopper communities in Sevilleta LTER, New Mexico, USA, we estimated lower abundance-based community change (smaller values of Bray–Curtis dissimilarity) when accounting for detection error (Figure 3). Potentially because of this reduction in Bray–Curtis dissimilarity, we estimated a weaker effect

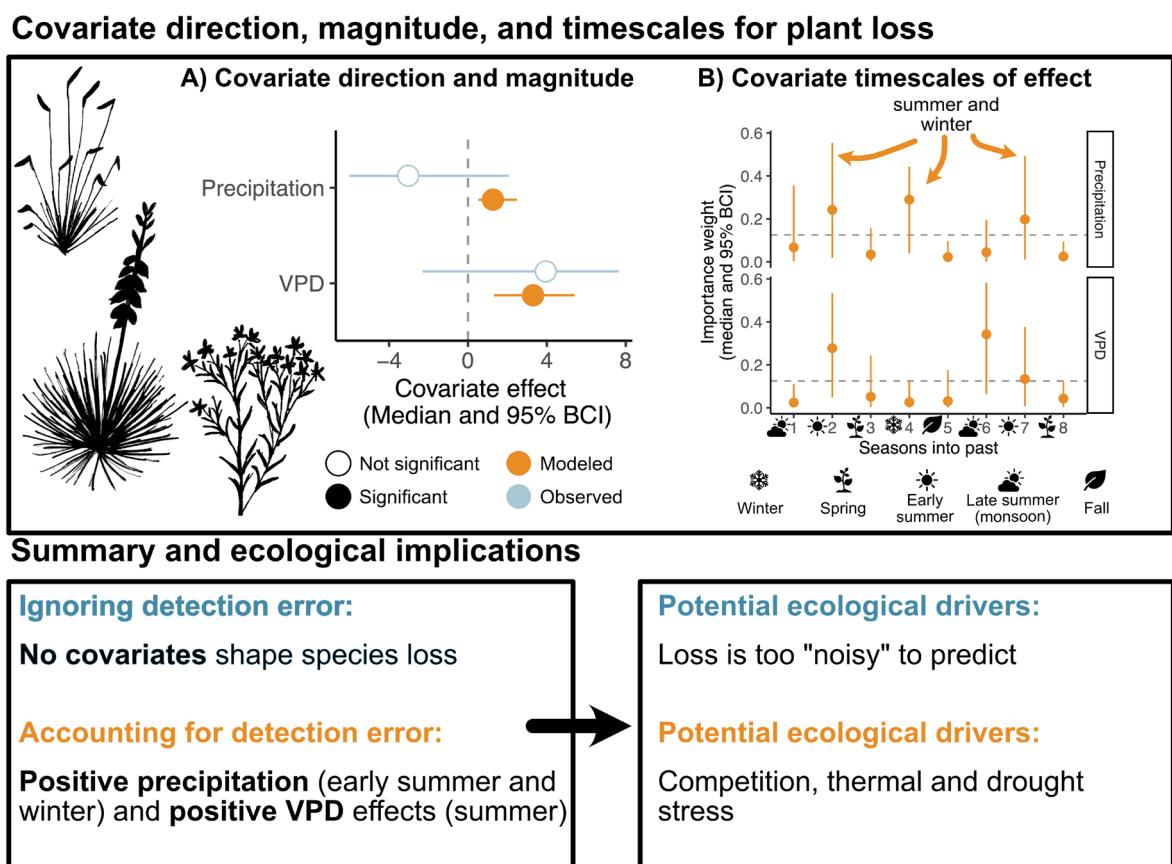
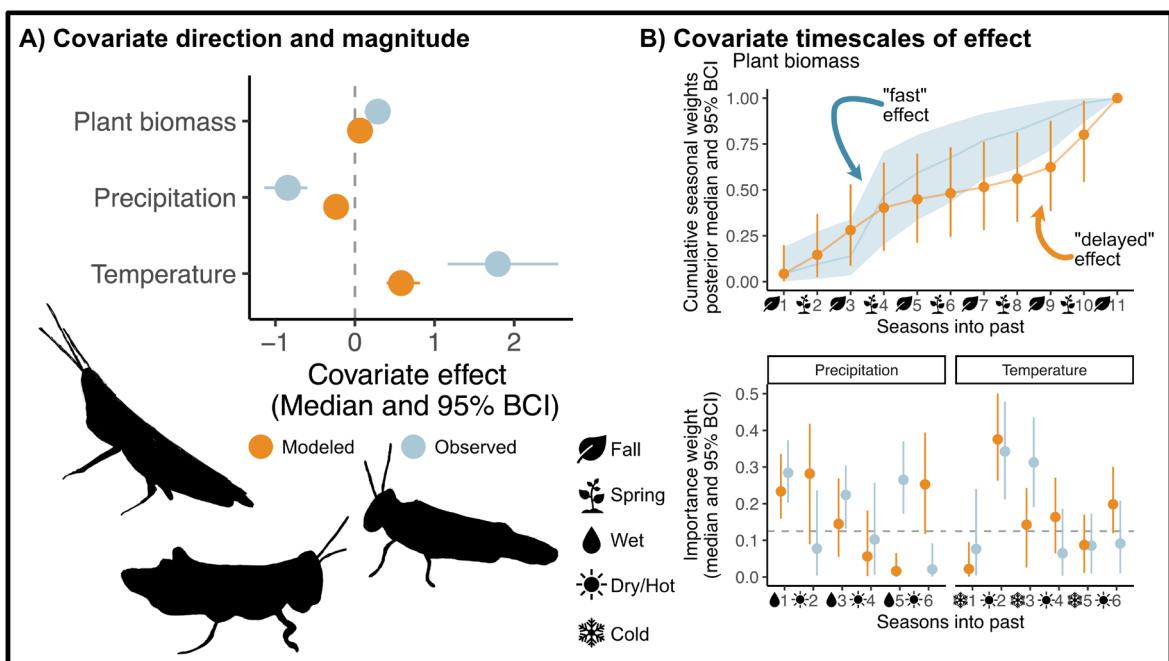


FIGURE 5 | Illustration of how accounting for imperfect detection alters estimates of covariate effects and timescales of influence on plant species loss for the Petrified Forest National Park, Arizona, USA understorey plant community (Swan and Plouffe 2023).

Covariate direction, magnitude, and timescales for grasshopper stability



Summary and ecological implications

Ignoring detection error:

Stronger effects of all covariates, fast response to plant biomass, wet season precipitation matters, longer temperature lag

Accounting for detection error:

Weaker effects of all covariates, delayed response to plant biomass, dry season precipitation matters, shorter temperature lag

Potential ecological drivers:

Competition for early-season resources, wet season growth and reproduction, longer thermal stress memory

Potential ecological drivers:

Competition following previous year growth, dry season growth and reproduction, short thermal stress memory

FIGURE 6 | Illustration of how accounting for imperfect detection alters estimates of covariate effects and time scales of influence on temporal dynamics of grasshopper communities based on Bray–Curtis dissimilarity. Data are from surveys of grasshopper species abundance from the Sevilleta Long-term Ecological Research (LTER) site, New Mexico, USA (Baur et al. 2022; Lightfoot 2021; Moore and Hall 2023). Accounting for imperfect detection alters estimates of covariate effects and time scales on temporal dynamics of grasshopper communities based on Bray–Curtis dissimilarity.

of all three covariates (precipitation, temperature, and plant biomass) on community change (Figure 6A). Further, we discovered shifts in the temporal signals of all covariates, including a shift to a more delayed effect of plant biomass, a change to a dry season precipitation signal (versus wet season), and a faster temperature signal (Figure 6B). Grasshopper community dynamics are driven by complex interactions among environmental drivers that vary across species with different food preferences and life histories (Branson 2008; Guo et al. 2009; Jonas et al. 2015). For example, a shift from wet to dry-season precipitation effects alters our interpretation of the ecological drivers in this system from responses to greater plant biomass due to high wet-season precipitation to a story of the importance of dry season precipitation on grasshopper abundance through alterations in plant nutritional quality (Branson 2017). That community change decreased when accounting for missed species and individuals suggests that rare species

may have important stabilizing effects in grasshopper communities. Further exploration of how temporal dynamics (Bray–Curtis dissimilarity) are shaped by the effects of abundance compensation across species and abundance gradients (e.g., Baselga 2013) may reveal the additional importance of rare species for patterns of community dynamics in these grasshopper communities.

3.4 | Conclusion: The Future of Tracking Biodiversity Change

The preceding examples showed that accounting for both the presence and abundance of rare species across communities and environments changed the direction, magnitude, and/or timescales of influence of global change drivers on biodiversity. These results alter our interpretation of potential mechanisms

that shape biodiversity change, which could lead to more focused experiments on the impacts of climate change on biodiversity across ecosystem types (Urban et al. 2016). Importantly, diversity responses were nuanced, highlighting the importance of community composition and the complex ecological interactions unique to every community. While we examined common global change drivers as mechanisms of change, this modeling approach could incorporate other biotic drivers (e.g., predation and competition) as potential drivers or mediators of biodiversity patterns (Hagen et al. 2012). Further, while we highlight a general beta regression method, any distribution appropriate for other stochastic “diversity index” types (e.g., Poisson for species richness, gaussian for Shannon diversity) can be incorporated into this modeling framework that propagates uncertainty. Variable effects of species detection on biodiversity metrics highlight that these metrics describe interrelated but distinct aspects of biological communities (Carroll et al. 2025). Further study of the unique responses of rare species to environmental change (e.g., Säterberg et al. 2019) is an important next step in this field.

We are likely in the Earth's sixth mass extinction (Cowie et al. 2022), which is characterized by an increased spatial scale and pace of biodiversity loss and change. It is imperative to understand how the reconfiguration of biological communities is shaping ecosystems across the globe. Not only are rare species more likely to go extinct (Harnik et al. 2012), but growing evidence, highlighted here and through our worked examples, illustrates how rare species can shape multiple facets of biodiversity (Mouillot et al. 2013; White et al. 2023), including those that impact ecosystem functioning. To best understand and predict how ongoing global change will continue to shape biodiversity, we suggest the need to examine multiple facets of biodiversity and not exclude subsets of communities from analyses based on faulty assumptions about their roles (or lack thereof) in shaping ecosystems. Building on growing literature on the importance of rare species to biodiversity and uniting modeling approaches already employed across disparate fields of ecology, we can better understand the relationships between biodiversity and our ever-changing planet.

Author Contributions

Ana Miller-ter Kuile: conceptualization, data curation, formal analysis, methodology, visualization, writing – original draft, writing – review and editing. **An Bui:** conceptualization, data curation, methodology, visualization, writing – original draft, writing – review and editing. **Austen Apigo:** conceptualization, methodology, validation, writing – review and editing. **Shelby Lamm:** data curation, formal analysis, visualization, writing – review and editing. **Megan Swan:** data curation, methodology, writing – original draft, writing – review and editing. **Jamie S. Sanderlin:** formal analysis, funding acquisition, methodology, supervision, writing – review and editing. **Kiona Ogle:** conceptualization, formal analysis, methodology, writing – original draft, writing – review and editing.

Acknowledgements

We thank the data managers at the Konza Prairie and Sevilleta LTERs for providing data for this study. AMtK was funded for this work under USDA Forest Service Agreement Challenge Cost Share 21-CS-11221635-194. Computational analyses were run on Northern Arizona University's Monsoon computing cluster, funded by Arizona's Technology and Research Initiative Fund. The views expressed in this

piece are those of the authors and do not represent official views of the USDA or Forest Service.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.15183897>. For the bird example from Konza Prairie LTER, bird and meteorological data were obtained from the Environmental Data Initiative Portal at <https://doi.org/10.6073/PASTA/17B63F19967D13BA55ACB5ED4D9601DE> and <https://doi.org/10.6073/PASTA/743C6B205E38A087BC54925ED258F549>, respectively. For the Petrified Forest National Park example, plant data were obtained from the National Park Service Data Store at <https://doi.org/10.57830/2300890> and climate data were obtained from PRISM at <https://prism.oregonstate.edu/>. For the Sevilleta LTER grasshopper example, grasshopper abundance, plant biomass, and climate data were obtained from the Environmental Data Initiative Portal at <https://doi.org/10.6073/PASTA/8DA81E91177DC6029D147990D1181BE3>, <https://doi.org/10.6073/PASTA/90F40FE4A7AB5ED5BCAB3527D6E9D84>, and <https://doi.org/10.6073/PASTA/DECDA0C695CB2070C73F5B684A32E73>, respectively.

References

- Anderson, M. J., T. O. Crist, J. M. Chase, et al. 2011. “Navigating the Multiple Meanings of β Diversity: A Roadmap for the Practicing Ecologist: Roadmap for Beta Diversity.” *Ecology Letters* 14, no. 1: 19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x>.
- Baselga, A. 2013. “Separating the Two Components of Abundance-Based Dissimilarity: Balanced Changes in Abundance vs. Abundance Gradients.” *Methods in Ecology and Evolution* 4, no. 6: 552–557. <https://doi.org/10.1111/2041-210X.12029>.
- Bateman, H. L., and D. Childers. 2024. “Long-Term Monitoring of Herpetofauna Along the Salt and Gila Rivers in and Near the Greater Phoenix Metropolitan Area, Ongoing Since 2012 [Dataset].” *Environmental Data Initiative*. <https://doi.org/10.6073/PASTA/BACF64544CDE50DC0C21F13B3614C587>.
- Baur, L., S. Collins, E. Muldavin, J. A. Rudgers, and W. T. Pockman. 2022. “SEV-LTER Quadrat Plant Species Biomass All Sites and Experiments.” *Environmental Data Initiative*. <https://doi.org/10.6073/PASTA/90F40FE4A7AB5ED5BCAB3527D6E9D84>.
- Botta-Dukát, Z. 2005. “Rao's Quadratic Entropy as a Measure of Functional Diversity Based on Multiple Traits.” *Journal of Vegetation Science* 16, no. 5: 533–540. <https://doi.org/10.1111/j.1654-1103.2005.tb02393.x>.
- Boyle, A. 2023. “CBP01 Variable Distance Line-Transect Sampling of Bird Population Numbers in Different Habitats on Konza Prairie.” *Environmental Data Initiative*. <https://doi.org/10.6073/PASTA/17B63F19967D13BA55ACB5ED4D9601DE>.
- Branson, D. H. 2008. “Influence of a Large Late Summer Precipitation Event on Food Limitation and Grasshopper Population Dynamics in a Northern Great Plains Grassland.” *Environmental Entomology* 37, no. 3: 686–695. [https://doi.org/10.1603/0046-225X\(2008\)37\[686:IOALLS\]2.0.CO;2](https://doi.org/10.1603/0046-225X(2008)37[686:IOALLS]2.0.CO;2).
- Branson, D. H. 2017. “Effects of Altered Seasonality of Precipitation on Grass Production and Grasshopper Performance in a Northern Mixed Prairie.” *Environmental Entomology* 46, no. 3: 589–594. <https://doi.org/10.1093/ee/nvx053>.
- Brasil, L. S., T. B. Vieira, A. F. A. Andrade, R. C. Bastos, L. F. D. A. Montag, and L. Juen. 2020. “The Importance of Common and the Irrelevance of Rare Species for Partition the Variation of Community

- Matrix: Implications for Sampling and Conservation." *Scientific Reports* 10, no. 1: 19777. <https://doi.org/10.1038/s41598-020-76833-5>.
- Broms, K. M., M. B. Hooten, and R. M. Fitzpatrick. 2015. "Accounting for Imperfect Detection in Hill Numbers for Biodiversity Studies." *Methods in Ecology and Evolution* 6, no. 1: 99–108. <https://doi.org/10.1111/2041-210X.12296>.
- Bruckerhoff, L. A., R. K. Connell, J. P. Guinnip, et al. 2020. "Harmony on the Prairie? Grassland Plant and Animal Community Responses to Variation in Climate Across Land-Use Gradients." *Ecology* 101, no. 5: e02986. <https://doi.org/10.1002/ecy.2986>.
- Cannon, P. G., J. J. Gilroy, J. A. Tobias, A. Anderson, T. Haugaasen, and D. P. Edwards. 2019. "Land-Sparing Agriculture Sustains Higher Levels of Avian Functional Diversity Than Land Sharing." *Global Change Biology* 25, no. 5: 1576–1590. <https://doi.org/10.1111/gcb.14601>.
- Carroll, K. A., A. M. Pidgeon, P. Elsen, L. Farwell, and V. C. Radeloff. 2025. "Biodiversity Metric Selection and Their Applications for Spatial Conservation Planning." *Diversity and Distributions* 31, no. 1: e13952. <https://doi.org/10.1111/ddi.13952>.
- Chao, A., R. L. Chazdon, R. K. Colwell, and T. Shen. 2005. "A New Statistical Approach for Assessing Similarity of Species Composition With Incidence and Abundance Data." *Ecology Letters* 8, no. 2: 148–159. <https://doi.org/10.1111/j.1461-0248.2004.00707.x>.
- Chen, G., M. Kéry, M. Plattner, K. Ma, and B. Gardner. 2013. "Imperfect Detection Is the Rule Rather Than the Exception in Plant Distribution Studies." *Journal of Ecology* 101, no. 1: 183–191. <https://doi.org/10.1111/1365-2745.12021>.
- Cowie, R. H., P. Bouchet, and B. Fontaine. 2022. "The Sixth Mass Extinction: Fact, Fiction or Speculation?" *Biological Reviews* 97, no. 2: 640–663. <https://doi.org/10.1111/brv.12816>.
- Cowles, J. M., P. D. Wragg, A. J. Wright, J. S. Powers, and D. Tilman. 2016. "Shifting Grassland Plant Community Structure Drives Positive Interactive Effects of Warming and Diversity on Aboveground Net Primary Productivity." *Global Change Biology* 22, no. 2: 741–749. <https://doi.org/10.1111/gcb.13111>.
- da Silva, P. G., M. I. M. Hernández, and J. Heino. 2018. "Disentangling the Correlates of Species and Site Contributions to Beta Diversity in Dung Beetle Assemblages." *Diversity and Distributions* 24, no. 11: 1674–1686. <https://doi.org/10.1111/ddi.12785>.
- Dee, L. E., J. Cowles, F. Isbell, S. Pau, S. D. Gaines, and P. B. Reich. 2019. "When Do Ecosystem Services Depend on Rare Species?" *Trends in Ecology & Evolution* 34, no. 8: 746–758. <https://doi.org/10.1016/j.tree.2019.03.010>.
- Devarajan, K., T. L. Morelli, and S. Tenan. 2020. "Multi-Species Occupancy Models: Review, Roadmap, and Recommendations." *EcoGraphy* 43, no. 11: 1612–1624. <https://doi.org/10.1111/ecog.04957>.
- Donoso, I., M. C. Sorensen, P. G. Blendinger, et al. 2020. "Downsizing of Animal Communities Triggers Stronger Functional Than Structural Decay in Seed-Dispersal Networks." *Nature Communications* 11, no. 1: 1582. <https://doi.org/10.1038/s41467-020-15438-y>.
- Dorazio, R. M., J. A. Royle, B. Söderström, and A. Glimskär. 2006. "Estimating Species Richness and Accumulation by Modeling Species Occurrence and Detectability." *Ecology* 87, no. 4: 842–854. [https://doi.org/10.1890/0012-9658\(2006\)87\[842:ESRAAB\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[842:ESRAAB]2.0.CO;2).
- Ellison, A. M. 2004. "Bayesian Inference in Ecology." *Ecology Letters* 7, no. 6: 509–520. <https://doi.org/10.1111/j.1461-0248.2004.00603.x>.
- Essl, F., S. Dullinger, W. Rabitsch, et al. 2015a. "Delayed Biodiversity Change: No Time to Waste." *Trends in Ecology & Evolution* 30, no. 7: 375–378. <https://doi.org/10.1016/j.tree.2015.05.002>.
- Essl, F., S. Dullinger, W. Rabitsch, et al. 2015b. "Historical Legacies Accumulate to Shape Future Biodiversity in an Era of Rapid Global Change." *Diversity and Distributions* 21, no. 5: 534–547. <https://doi.org/10.1111/ddi.12312>.
- Fernández-Pascual, E., E. Mattana, and H. W. Pritchard. 2019. "Seeds of Future Past: Climate Change and the Thermal Memory of Plant Reproductive Traits." *Biological Reviews* 94, no. 2: 439–456. <https://doi.org/10.1111/brv.12461>.
- Ferrari, S., and F. Cribari-Neto. 2004. "Beta Regression for Modelling Rates and Proportions." *Journal of Applied Statistics* 31, no. 7: 799–815. <https://doi.org/10.1080/0266476042000214501>.
- Figueiredo, L., J. Krauss, I. Steffan-Dewenter, and J. Sarmento Cabral. 2019. "Understanding Extinction Debts: Spatio-Temporal Scales, Mechanisms and a Roadmap for Future Research." *EcoGraphy* 42, no. 12: 1973–1990. <https://doi.org/10.1111/ecog.04740>.
- Garrard, G. E., M. A. McCarthy, N. S. G. Williams, S. A. Bekessy, and B. A. Wintle. 2013. "A General Model of Detectability Using Species Traits." *Methods in Ecology and Evolution* 4, no. 1: 45–52. <https://doi.org/10.1111/j.2041-210x.2012.00257.x>.
- Gibb, H., R. R. Dunn, N. J. Sanders, et al. 2017. "A Global Database of Ant Species Abundances." *Ecology* 98, no. 3: 883–884. <https://doi.org/10.1002/ecy.1682>.
- Guo, K., S. Hao, O. J. Sun, and L. Kang. 2009. "Differential Responses to Warming and Increased Precipitation Among Three Contrasting Grasshopper Species." *Global Change Biology* 15, no. 10: 2539–2548. <https://doi.org/10.1111/j.1365-2486.2009.01861.x>.
- Hagen, M., W. D. Kissling, C. Rasmussen, et al. 2012. "Biodiversity, Species Interactions and Ecological Networks in a Fragmented World." In *Advances in Ecological Research*, vol. 46, 89–210. Elsevier. <https://doi.org/10.1016/B978-0-12-396992-7.00002-2>.
- Hallett, L. M., S. K. Jones, A. A. M. MacDonald, et al. 2016. "CODYN: An R Package of Community Dynamics Metrics." *Methods in Ecology and Evolution* 7, no. 10: 1146–1151. <https://doi.org/10.1111/2041-210X.12569>.
- Harnik, P. G., C. Simpson, and J. L. Payne. 2012. "Long-Term Differences in Extinction Risk Among the Seven Forms of Rarity." *Proceedings of the Royal Society B: Biological Sciences* 279, no. 1749: 4969–4976. <https://doi.org/10.1098/rspb.2012.1902>.
- Iknayan, K. J., M. W. Tingley, B. J. Furnas, and S. R. Beissinger. 2014. "Detecting Diversity: Emerging Methods to Estimate Species Diversity." *Trends in Ecology & Evolution* 29, no. 2: 97–106. <https://doi.org/10.1016/j.tree.2013.10.012>.
- Illán, J. G., C. D. Thomas, J. A. Jones, W. Wong, S. M. Shirley, and M. G. Betts. 2014. "Precipitation and Winter Temperature Predict Long-Term Range-Scale Abundance Changes in Western North American Birds." *Global Change Biology* 20, no. 11: 3351–3364. <https://doi.org/10.1111/gcb.12642>.
- Irvine, K. M., T. J. Rodhouse, and I. N. Keren. 2016. "Extending Ordinal Regression With a Latent Zero-Augmented Beta Distribution." *Journal of Agricultural, Biological and Environmental Statistics* 21, no. 4: 619–640. <https://doi.org/10.1007/s13253-016-0265-2>.
- Jain, M., D. F. B. Flynn, C. M. Prager, et al. 2014. "The Importance of Rare Species: A Trait-Based Assessment of Rare Species Contributions to Functional Diversity and Possible Ecosystem Function in Tall-Grass Prairies." *Ecology and Evolution* 4, no. 1: 104–112. <https://doi.org/10.1002/ece3.915>.
- Jaureguiberry, P., N. Titeux, M. Wiemers, et al. 2022. "The Direct Drivers of Recent Global Anthropogenic Biodiversity Loss." *Science Advances* 8, no. 45: eabm9982. <https://doi.org/10.1126/sciadv.abm9982>.
- Jeliazkov, A., Y. Gavish, C. J. Marsh, et al. 2022. "Sampling and Modelling Rare Species: Conceptual Guidelines for the Neglected Majority." *Global Change Biology* 28, no. 12: 3754–3777. <https://doi.org/10.1111/gcb.16114>.
- Jonas, J. L., W. Wolessensky, and A. Joern. 2015. "Weather Affects Grasshopper Population Dynamics in Continental Grassland Over

- Annual and Decadal Periods." *Rangeland Ecology & Management* 68, no. 1: 29–39. <https://doi.org/10.1016/j.rama.2014.12.011>.
- Kadmon, R. 1995. "Plant Competition Along Soil Moisture Gradients: A Field Experiment With the Desert Annual *Stipa capensis*." *Journal of Ecology* 83, no. 2: 253. <https://doi.org/10.2307/2261564>.
- Kellner, K. F., and R. K. Swihart. 2014. "Accounting for Imperfect Detection in Ecology: A Quantitative Review." *PLoS One* 9, no. 10: e111436. <https://doi.org/10.1371/journal.pone.0111436>.
- Kéry, M., and B. Schmidt. 2008. "Imperfect Detection and Its Consequences for Monitoring for Conservation." *Community Ecology* 9, no. 2: 207–216. <https://doi.org/10.1556/comec.9.2008.2.10>.
- Kokko, H. 1999. "Competition for Early Arrival in Migratory Birds." *Journal of Animal Ecology* 68, no. 5: 940–950. <https://doi.org/10.1046/j.1365-2656.1999.00343.x>.
- Lamouille-Hébert, M., F. Arthaud, A. Besnard, M. Logez, and T. Datry. 2025. "Increased Drying Threatens Alpine Pond Biodiversity More Than Temperature Increase in a Changing Climate." *Aquatic Sciences* 87, no. 1: 25. <https://doi.org/10.1007/s00027-024-01155-x>.
- Leitão, R. P., J. Zuanon, S. Villéger, et al. 2016. "Rare Species Contribute Disproportionately to the Functional Structure of Species Assemblages." *Proceedings of the Royal Society B: Biological Sciences* 283, no. 1828: 20160084. <https://doi.org/10.1098/rspb.2016.0084>.
- Lightfoot, D. 2021. "Long-Term Core Site Grasshopper Dynamics for the Sevilleta National Wildlife Refuge, New Mexico." *Environmental Data Initiative*. <https://doi.org/10.6073/PASTA/8DA81E91177DC6029D147990D1181BE3>.
- Loreau, M., and C. de Mazancourt. 2013. "Biodiversity and Ecosystem Stability: A Synthesis of Underlying Mechanisms." *Ecology Letters* 16, no. s1: 106–115. <https://doi.org/10.1111/ele.12073>.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. "Estimating Site Occupancy Rates When Detection Probabilities Are Less Than One." *Ecology* 83, no. 8: 2248–2255. [https://doi.org/10.1890/0012-9658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2).
- Mammola, S., C. P. Carmona, T. Guillerme, and P. Cardoso. 2021. "Concepts and Applications in Functional Diversity." *Functional Ecology* 35, no. 9: 1869–1885. <https://doi.org/10.1111/1365-2435.13882>.
- Marra, P. P., C. M. Francis, R. S. Mulvihill, and F. R. Moore. 2005. "The Influence of Climate on the Timing and Rate of Spring Bird Migration." *Oecologia* 142, no. 2: 307–315. <https://doi.org/10.1007/s00442-004-1725-x>.
- Matthies, D., I. Bräuer, W. Maibom, and T. Tscharntke. 2004. "Population Size and the Risk of Local Extinction: Empirical Evidence From Rare Plants." *Oikos* 105, no. 3: 481–488. <https://doi.org/10.1111/j.0030-1299.2004.12800.x>.
- McKinnon, L., M. Picotin, E. Bolduc, C. Juillet, and J. Béty. 2012. "Timing of Breeding, Peak Food Availability, and Effects of Mismatch on Chick Growth in Birds Nesting in the High Arctic." *Canadian Journal of Zoology* 90, no. 8: 961–971. <https://doi.org/10.1139/z2012-064>.
- Miller-ter Kuile, A., S. Lamm, and A. Bui. 2025. "Anamtk/community_detection: V4 (Version v4)." *Zenodo*. <https://doi.org/10.5281/ZENODO.15183897>.
- Moore, D. I., and K. M. Hall. 2023. "Meteorology Data From the Sevilleta National Wildlife Refuge, New Mexico." *Environmental Data Initiative*. <https://doi.org/10.6073/PASTA/DECDAAC0C695CB2070C73F5B684A32E73>.
- Morgan Ernest, S. K., J. H. Brown, T. J. Valone, M. J. Culshaw-Maurer, and E. P. White. 2022. "Ratdat: Portal Project Teaching Database (Version 1.0.0)." <https://CRAN.R-project.org/package=ratdat>.
- Morris, E. K., T. Caruso, F. Buscot, et al. 2014. "Choosing and Using Diversity Indices: Insights for Ecological Applications From the German Biodiversity Exploratories." *Ecology and Evolution* 4, no. 18: 3514–3524. <https://doi.org/10.1002/ece3.1155>.
- Mouillot, D., D. R. Bellwood, C. Baraloto, et al. 2013. "Rare Species Support Vulnerable Functions in High-Diversity Ecosystems." *PLoS Biology* 11, no. 5: e1001569. <https://doi.org/10.1371/journal.pbio.1001569>.
- Nippert, J. 2023. "AWE01 Meteorological Data From the Konza Prairie Headquarters Weather Station." *Environmental Data Initiative*. <https://doi.org/10.6073/PASTA/743C6B205E38A087BC54925ED258F549>.
- Ogle, K., J. Barber, and K. Sartor. 2013. "Feedback and Modularization in a Bayesian Meta-Analysis of Tree Traits Affecting Forest Dynamics." *Bayesian Analysis* 8, no. 1: 133. <https://doi.org/10.1214/13-BA806>.
- Ogle, K., J. J. Barber, G. A. Barron-Gafford, et al. 2015. "Quantifying Ecological Memory in Plant and Ecosystem Processes." *Ecology Letters* 18, no. 3: 221–235. <https://doi.org/10.1111/ele.12399>.
- Oksanen, J., F. Guillaume Blanchet, M. Friendly, et al. 2020. "Vegan: Community Ecology Package (Version 2.5-7)." <https://CRAN.R-project.org/package=vegan>.
- Poos, M. S., and D. A. Jackson. 2012. "Addressing the Removal of Rare Species in Multivariate Bioassessments: The Impact of Methodological Choices." *Ecological Indicators* 18: 82–90. <https://doi.org/10.1016/j.ecolind.2011.10.008>.
- PRISM Climate Group. 2014. "PRISM." <https://prism.oregonstate.edu>.
- Rabinowitz, D. 1981. "Seven Forms of Rarity." In *Foundations in Macroecology*, 480. University of Chicago Press.
- Reed, D. C., and R. J. Miller. 2022. "SBC LTER: Reef: Kelp Forest Community Dynamics: Fish Abundance." *Environmental Data Initiative*. <https://doi.org/10.6073/PASTA/E0270D5A617339F91AE518C99EB67FDA>.
- Roth, T., E. Allan, P. B. Pearman, and V. Amrhein. 2018. "Functional Ecology and Imperfect Detection of Species." *Methods in Ecology and Evolution* 9, no. 4: 917–928. <https://doi.org/10.1111/2041-210X.12950>.
- Royle, J. A., J. D. Nichols, and M. Kéry. 2005. "Modelling Occurrence and Abundance of Species When Detection Is Imperfect." *Oikos* 110, no. 2: 353–359. <https://doi.org/10.1111/j.0030-1299.2005.13534.x>.
- Sanderlin, J. S., W. M. Block, and J. L. Ganey. 2014. "Optimizing Study Design for Multi-Species Avian Monitoring Programmes." *Journal of Applied Ecology* 51, no. 4: 860–870. <https://doi.org/10.1111/1365-2664.12252>.
- Sasaki, T., and W. K. Lauenroth. 2011. "Dominant Species, Rather Than Diversity, Regulates Temporal Stability of Plant Communities." *Oecologia* 166, no. 3: 761–768. <https://doi.org/10.1007/s00442-011-1916-1>.
- Säterberg, T., T. Jonsson, J. Yearsley, S. Berg, and B. Ebenman. 2019. "A Potential Role for Rare Species in Ecosystem Dynamics." *Scientific Reports* 9, no. 1: 11107. <https://doi.org/10.1038/s41598-019-47541-6>.
- Si, X., M. W. Cadotte, Y. Zhao, et al. 2018. "The Importance of Accounting for Imperfect Detection When Estimating Functional and Phylogenetic Community Structure." *Ecology* 99, no. 9: 2103–2112. <https://doi.org/10.1002/ecy.2438>.
- Studds, C. E., and P. P. Marra. 2011. "Rainfall-Induced Changes in Food Availability Modify the Spring Departure Programme of a Migratory Bird." *Proceedings of the Royal Society B: Biological Sciences* 278, no. 1723: 3437–3443. <https://doi.org/10.1098/rspb.2011.0332>.
- Swan, M., and L. Ploughe. 2023. "SCPN UplandVegetation Herbaceous and Shrub Vegetation and Soils 2007–2022 Data Package." *National Park Service*. <https://doi.org/10.57830/2300890>.

- Thompson, P. M., and J. C. Ollason. 2001. "Lagged Effects of Ocean Climate Change on Fulmar Population Dynamics." *Nature* 413, no. 6854: 417–420. <https://doi.org/10.1038/35096558>.
- Tingley, M. W., C. P. Nadeau, and M. E. Sandor. 2020. "Multi-Species Occupancy Models as Robust Estimators of Community Richness." *Methods in Ecology and Evolution* 11, no. 5: 633–642. <https://doi.org/10.1111/2041-210X.13378>.
- Tobias, J. A., C. Sheard, A. L. Pigot, A. J. M. Devenish, J. Yang, and F. Sayol. 2022. "AVONET: Morphological, Ecological and Geographical Data for All Birds." *Ecology Letters* 25, no. 3: 581–597. <https://doi.org/10.1111/ele.13898>.
- Urban, M. C., G. Bocedi, A. P. Hendry, J.-B. Mihoub, G. Peer, and A. Singer. 2016. "Improving the Forecast for Biodiversity Under Climate Change." *Science* 353, no. 6304: aad8466. <https://doi.org/10.1126/science.aad8466>.
- Walter, J., L. Nagy, R. Hein, et al. 2011. "Do Plants Remember Drought? Hints Towards a Drought-Memory in Grasses." *Environmental and Experimental Botany* 71, no. 1: 34–40. <https://doi.org/10.1016/j.envexpbot.2010.10.020>.
- White, H. J., C. M. McKeon, R. J. Pakeman, and Y. M. Buckley. 2023. "The Contribution of Geographically Common and Rare Species to the Spatial Distribution of Biodiversity." *Global Ecology and Biogeography* 32, no. 10: 1730–1747. <https://doi.org/10.1111/geb.13734>.
- Zipkin, E. F., J. Andrew Royle, D. K. Dawson, and S. Bates. 2010. "Multi-Species Occurrence Models to Evaluate the Effects of Conservation and Management Actions." *Biological Conservation* 143, no. 2: 479–484. <https://doi.org/10.1016/j.biocon.2009.11.016>.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.